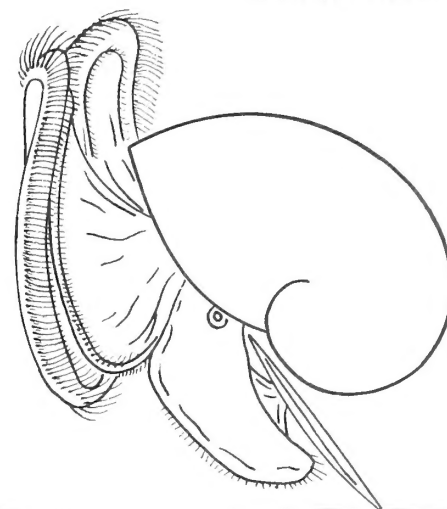


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Systematics and Phylogeny of *Philine* (Gastropoda: Opisthobranchia), with Emphasis on the *Philine aperta* Species Complex

REBECCA M. PRICE

Interdisciplinary Arts and Sciences, University of Washington, Bothell, Box 358511, 18115 Campus Way NE,
Bothell, WA 98011-8246, USA

TERRENCE M. GOSLINER

Department of Invertebrate Zoology and Geology, California Academy of Sciences, 55 Music Concourse Drive, San
Francisco, CA 94118, USA

AND

ÁNGEL VALDÉS

Department of Biological Sciences, California State Polytechnic University, 3801 West Temple Avenue, Pomona,
CA 91768-4032, USA

Abstract. This study includes detailed morphological examination of 16 species of *Philine* to reconstruct a phylogenetic hypothesis of relationships within the Philinidae. Our purpose is to test the monophyly of a complex of species that closely resemble the type species, *Philine aperta* (Linnaeus, 1767). Our cladistic analysis of *Philine* supports both the monophyly of the genus and of a subclade of the *Philine aperta* clade. This *P. aperta* subclade consists of highly derived species that serve as poor models for understanding plesiomorphic attributes within the genus *Philine* and also within the family Philinidae; aspects of their morphology are too highly modified to provide appropriate exemplars of evolution of the entire clade. The systematics of this subclade has long been confused because of only subtle, but consistent, differences between species. Consequently, species have been synonymized and separated repeatedly. We found several characters of systematic importance that had not been used previously, including microstructure of the gizzard plates, fine details of the penial papilla, and branching of the prostate complex. We describe each of the taxa in the *P. aperta* clade that we examined, including the first detailed description of *Philine orientalis* A. Adams, 1854, and the first anatomical description of *Philine elegans* Bergh, 1905. We also describe four new species in the *Philine aperta* clade: *Philine fenestra* sp. nov., *Philine paucipapillata* sp. nov., *Philine puka* sp. nov., and *Philine sarcophaga* sp. nov. Specimens identified as *Philine orientalis* A. Adams, 1854 from Hong Kong (Morton & Chiu, 1990) and Cambodia (present study) are morphologically distinct from those found elsewhere (present study) and represent a distinct species described here as *P. paucipapillata* sp. nov. Lastly, we redescribe *Philine alba* Mattox, 1958, from California and differentiate it from the specimens of *P. alba* from several localities in the Western Atlantic described by Marcus & Marcus (1967) and Marcus (1974). We erect the name *P. alboideus* sp. nov. for the Marcuses' specimens.

INTRODUCTION

The genus *Philine* Ascanius, 1772 contains at least 90 species, not including synonyms (Rudman, 1972b), making it among the most species-rich genera of opisthobranchs. The systematic boundaries of many species and nominal genera have been the source of considerable confusion; this confusion is exacerbated by several of these species having been recently introduced by international shipping, probably through discharge of ballast water (Gosliner, 1995; Gosliner & Williams, 2007). It is imperative to have reliable

systematic and morphological data available both to resources managers and systematists.

Unfortunately, most species are known only from their shells. This has created considerable taxonomic confusion and misidentifications of taxa, owing to the convergent shell morphology within this group. Species with similar shells often have dramatic differences in internal anatomy. For example, there has been confusion surrounding the identity of the two large, shallow-water species that have been introduced into San Francisco Bay (Gosliner, 1995; Rudman, 1998b; Gosliner & Williams, 2007). Recently, one of our

colleagues, who has considerably more experience in studying details of shell structure, misidentified shells of one introduced species as *Philine argentata* Gould, 1860 despite the fact that this species has gizzard plates that are radically different from those of the species he was considering. So strong is convergence in shell morphology between taxa that it cannot be considered by itself to constitute a reliable basis for differentiating species. Although shell characters are informative to a degree, we strongly discourage the practice of basing new taxa exclusively upon shell morphology, because it further exacerbates the systematic confusion within this diverse group of species. Presently, fossil taxa cannot be included in an analysis of fine-level species differences because other key morphological features are unknown.

Despite the challenges associated with using shell characters in this group, the anatomy remains unknown for the majority of known *Philine* species. Many morphological descriptions of *Philine* species have been undertaken over the past several decades (Marcus & Marcus, 1966, 1967, 1969; Rudman, 1970, 1972a, b; Gosliner, 1988), and these studies describe new taxa and review the anatomy of previously identified species. In one of these studies, Guiart (1901:107; fig. 59) presents an excellent drawing of the overall anatomy and body plan of *Philine* with his depiction of the anatomy of *Philine quadripartita* (as *P. aperta*). Still, the anatomy is known only from approximately one third of the identified species of *Philine*. This difficulty precludes a monographic review that studies the majority of *Philine* species. Thus, this article is not a monographic review of *Philine*, nor is it meant to be a comprehensive test of the monophyly of all generic names applied to taxa within the Philinidae. Such work is not possible at this time, because many of the type species are known only from shells and cannot be studied in a comprehensive phylogenetic analysis.

We find that, within *Philine*, most of the systematically informative variation is internal; the external features have been considered uniform throughout the genus. Most animals are white. The body is composed of cephalic and posterior shields flanked by relatively narrow parapodial lobes. Interspecific variations of the gizzard plates, penis and prostate complex, shell structure and sculpture, and radular formula have been used as criteria for subdividing the genus (Lemche, 1948; Habe, 1950; Marcus, 1974), but none of these criteria have been tested with a cladistic framework. Consequently, many of the genera are monotypic, do not divide the genus into monophyla, and are not accepted by other authors (Rudman, 1972b; Gosliner, 1988).

This article consolidates the current state of knowledge for the external and internal anatomy of well-described species of *Philine* to identify well-defined clades to begin recognizing well-supported groups so

that future studies can refine *Philine* systematics. We focus on the anatomy of species that are members of the *Philine aperta* species complex, in which the prostate gland has complex secondary branching and the gizzard plates are ornamented with pores or other structures. As we embarked on this study, we found that subtle and consistent differences in anatomy do exist among species in the *P. aperta* species complex that had been synonymized previously. After conducting a phylogenetic analysis that includes all the known members of this complex and 11 additional species in the genus, we found that these subtleties are synapomorphies that confirm that the *P. aperta* species complex is a clade. The taxa included in the analysis represent the entire known range of anatomical variation within *Philine*. In addition, two outgroup taxa, *Scaphander mundus* Watson, 1883 and *Cyllichna alba* (Brown, 1827) were included.

This article also describes several new species and constructs a preliminary phylogenetic hypothesis to determine monophyly of *Philine* and clades within the Philinidae.

MATERIALS AND METHODS

Material examined: The material examined is deposited at the following institutions: California Academy of Sciences, San Francisco, California, USA (CASIZ); The Natural History Museum, London, United Kingdom (BMNH); Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM); Iziko South African Museum, Cape Town, South Africa (SAM); and the Museum National d'Histoire Naturelle, Paris, France (MNHN).

Morphological study: We begin by discussing the type species, *P. aperta*, and the rest of the species are discussed and arranged alphabetically by species name. Features of living animals were recorded from photographs and notes by collectors. The specimens were dissected by ventral and dorsal incision to facilitate morphological examination. The internal features were examined using a dissecting microscope and drawn with the aid of a camera lucida. Special attention was paid to the morphology of the reproductive system, including the detailed anatomy of the penial papilla and prostate. The buccal mass was dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. Gizzard plates were removed by dissection and rinsed in deionized water, dried, and mounted on electron microscopy stubs. The radula was then also rinsed in water, dried, and mounted for examination by scanning electron microscopy (SEM). In addition to anatomical information collected by direct examination of specimens during this study,

Table 1
Literature used to study *Philine* species included in our phylogenetic analysis

Species	Literature
<i>P. alba</i> Mattox, 1958	Mattox, 1958; Marcus and Marcus, 1967; Marcus, 1974; present study
<i>P. "alba"</i> (called <i>P. alboides</i> herein)	Marcus and Marcus, 1967; Marcus, 1974; present study
<i>P. angasi</i> (Crosse & Fischer, 1865)	Rudman, 1970, 1972a, 1998b; present study
<i>P. aperta</i> (Linnaeus, 1767)	Bergh, 1907; Brown, 1934; Hurst, 1965; Marcus and Marcus, 1966; Horikoshi, 1967; Marcus, 1974; Thompson, 1976; present study
<i>P. argentata</i> Gould, 1860, a synonym of <i>P. orientalis</i>	Habe, 1950; Morton and Chiu, 1990; Higo et al., 1999; present study
<i>P. auriformis</i> Suter, 1909	Rudman, 1970, 1972a, b; Gosliner, 1995; present study
<i>P. babai</i> Valdés, 2008	Valdés, 2008; present study
<i>P. berghi</i> E. A. Smith, 1910	Bergh, 1907; O'Donoghue, 1929
<i>P. elegans</i> Bergh, 1905	Bergh, 1905; present study
<i>P. falklandica</i> Powell, 1954	Rudman, 1972a; present study
<i>P. fenestra</i> Price, Gosliner, and Valdés, n. sp.	Present study
<i>P. finmarchica</i> Sars, 1858	Lemche, 1948; Marcus and Marcus, 1969; Marcus, 1974; present study
<i>P. gibba</i> Strebel, 1908	Marcus and Marcus, 1969; Rudman, 1972a; Seager, 1978; present study
<i>P. habei</i> Valdés, 2008	Valdés, 2008; present study
<i>P. infundibulum</i> Dall, 1889	Marcus and Marcus, 1967; Marcus, 1974; present study
<i>P. lima</i> (Brown, 1825)	Lemche, 1948; Marcus and Marcus, 1969; present study
<i>P. orca</i> Gosliner, 1988	Gosliner, 1988; Baba, 1990
<i>P. "orientalis"</i> A. Adams, 1854, called <i>P. paucipapillata</i> herein	Morton and Chiu, 1990; present study
<i>P. pruinosa</i> (Clark, 1827)	Lemche, 1948; Thompson, 1976; Morton and Chiu, 1990
<i>P. puka</i> Price, Gosliner, and Valdés, n. sp.	Present study
<i>P. quadrata</i> (Wood, 1839)	Lemche, 1948; Horikoshi, 1967; Marcus and Marcus, 1969; Rudman, 1972a; Thompson, 1976; present study
<i>P. quadripartita</i> (Ascanius, 1772)	Bergh, 1901, 1905; Brown, 1934; Hurst, 1965; Horikoshi, 1967; Thompson, 1976; present study
<i>P. rubrata</i> Gosliner, 1988	Gosliner, 1988; Baba, 1990
<i>P. sarcophaga</i> Price, Gosliner, and Valdés, n. sp.	Present study
<i>P. t. thurmanni</i> Marcus and Marcus, 1969	Marcus and Marcus, 1969
<i>S. kensleyi</i> Gosliner, 1988	Gosliner, 1988
<i>C. alba</i> (Braun, 1827)	Lemche, 1956
<i>S. mundus</i> Watson, 1833	Marcus and Marcus, 1966; Marcus, 1974

morphological data were augmented by prior publications on the anatomy of species of *Philine* (Table 1).

Phylogenetic analysis: To calculate the most parsimonious phylogenetic trees, data were analyzed with Phylogenetic Analysis Using Parsimony (PAUP*), version 4.0b10 (Swofford, 2002), by using the heuristic algorithm (Branch swapping option [TBR]). In cases in which a taxon had two states for a given character, they were treated as uncertain. Both the accelerated transformation (ACCTRAN) and the delayed transformation (DELTRAN) optimizations were used for character transformation. In both cases, the analyses were performed treating the characters as unordered. One thousand random starting trees were obtained via stepwise addition. The trees were rooted using *C. alba* and *S. mundus* as outgroups. In successive analyses, each outgroup taxon was used as the only outgroup, and in other analyses both taxa (*C. alba* and *S. mundus*) were used as an outgroup. The resulting trees did not

vary in topology. Both of these taxa have several attributes (such as a less detorted body and a more well-developed shell) that suggest that they are more plesiomorphic in many aspects of their anatomy, and they are thought to be close basal relatives of the philinids (Mikkelsen, 1996). A decay analysis using a heuristic search by PAUP* was conducted to estimate branch support. Synapomorphies were mapped using the character trace option in MacClade 4.08 (Maddison & Maddison, 2005) based on the strict consensus tree from the PAUP* analysis.

SPECIES DESCRIPTIONS

Family PHILINIDAE Gray, 1850

Philine Ascanius, 1772:329.

Type species: *Bulla aperta* Linnaeus, 1767 by monotypy.

Diagnosis: Divided body consisting of cephalic and posterior shields. Posterior shield contains internalized shell. Distinct parapodial lobes (Figure 1A). Jaw rodlets absent. Radular formula 0-6.1.0-1.1.0-6. Rachidian tooth reduced or absent. Inner lateral teeth usually denticulate. Gizzard plates three, equal or unequal in size, that are not covered by muscles (Figure 1B). Reproductive system monaulic. Ciliated sperm groove along right side. Penis simple or complex. Euthyneurous nervous system with elongate visceral loop.

Philine aperta (Linnaeus, 1767)

(Figures 2A, B; 3; 4)

Bulla aperta Linnaeus, 1767:1183.

Philine aperta (Linnaeus, 1767) Bergh, 1907:24, pl. 5, figs. 5-10.

Bullaea capensis Pfeiffer, 1840. Bergh, 1907:24.

Bulla schroeteri Philippi, 1844:94, pl. 20, fig. 2; Bergh, 1907:24.

Philine capensis O'Donoghue, 1929:10.

Philine aperta guiniensis Marcus and Marcus, 1966:159, figs. 9-18. Marcus, 1974:360, fig. 104.

Material: SAM A54287, University of Cape Town Ecological Survey, Station NAD 75, one specimen, 30 mm, coarse sand, 38 m depth, 29°19.8'S, 31°26.2'E, September 10, 1964. SAM A54286, University of Cape Town Ecological Survey, Station NAD 59B, one specimen, dissected, 42 mm, green mud, 77 m depth, 29°26'S, 31°46.2'E, September 9, 1964. SAM, University of Cape Town Ecological Survey, Station FAL 786 L, one specimen, dissected, 20 mm, coarse sand and shell, 27 m depth, 34°17.0'S, 18°29.2'E, February 15, 1965. SAM, University of Cape Town Ecological Survey, Station FAL 743 Q, one specimen, 9 mm, coarse sand and shell, 7 m depth, 34°09.5'S, 18°50.6'E, February 16, 1965. SAM, University of Cape Town Ecological Survey, Station FB 402A, False Bay, South Africa, two specimens, 6-9 mm, fine sand, 31 m depth, 34°8.8'S, 18°33.5'E, May 16, 1961. SAM A54288, University of Cape Town Ecological Survey, Station SCD 189D, False Bay, South Africa, three specimens, 2 dissected, 40-60 mm, fine sand, 10 m depth, 34°05.8'S, 23°23.2'E, November 29, 1960.

Distribution: Known from Saldanha Bay (South Africa) to Mozambique.

Natural history: This species is found in relatively shallow water from 3 to 100 m depth in coarse sandy substrate. The egg masses (Figure 2B) are elongate sacs that are attached to the sand by a mucous thread.

External morphology: The living animal is uniformly white to yellowish (Figure 2A), ranging in size from approximately 1 to 6 cm. The cephalic shield is longer

than the posterior shield (Figure 3A). The parapodial lobes are thick and muscular, and the posterior notch is shallow.

Internal morphology: The shell is relatively tightly coiled, and its surface lacks sculpture.

There is a single, short, ventral oral gland, and there are two dorsal oral glands. The buccal bulb and radula are reduced; the radular formula is 16-20 × 1.0.1. The inner lateral tooth is broad with 37-51 denticles (Figure 4C). The crop is indistinct. Although the gizzard is muscularized, the plates are not covered with muscles. The esophagus passes directly through the three large gizzard plates. The plates are spindle-shaped, and each has two medium-sized pores (Figure 4A, B). The paired plates (e.g., Figure 4A) are larger than the unpaired plate (Figure 4B). The gizzard-plate microsculpture consists of circular indentations, within which there is a finely meshed subsculpture (Figure 4D). The salivary glands are short.

The fused pleural-parietal ganglion can be adjacent to or can adjoin the anterior suprainestinal ganglion. The genital ganglion is fused to the visceral ganglion. The subintestinal ganglion is adjacent to the fused visceral and genital ganglia.

The penial papilla is hammer-shaped with subequal lobes, fitting within the penial sac without distending it (Figure 3B). The convoluted prostate branches to the ejaculatory duct, and a short muscle connects the end of the prostate to the sac (Figure 3C). The ejaculatory duct is short.

The convoluted ampulla narrows to the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 3D). The mucous gland is large, and it bends at the free end. There is a secondary bursa copulatrix at the base of the spherical, thin-walled, primary bursa copulatrix.

Discussion: The gizzard plates of *P. aperta* are shaped like "tricornered hats" (Marcus, 1974:347) with medium-sized pores. These plates look most similar to those in *Philine orientalis*, *P. quadripartita*, and especially *Philine paucipapillata*. The plates of *Philine angasi* and *Philine elegans* are similar, but they are also twisted, and more concave. *Philine puka* also has plates with the tricornered hat shape, but it has large pores. The gizzard-plate microstructure is most like that in *P. angasi* and *P. paucipapillata*.

The penial morphology of *P. aperta* is distinct because of the wide penial sac and the three long lobes. The hammer head is closely appressed to the anterior of the sac. It is most similar in shape to the hammer heads of *P. orientalis* and *P. quadripartita*.

The narrow posterior portion of the cephalic shield is similar to that of *Philine angasi*, *P. argentata*, *P. orientalis*, *P. paucipapillata*, and *P. puka*.

Bergh (1901) and Lemche (1948) synonymized the European *P. quadripartita* with the African *P. aperta*. Marcus & Marcus (1966) distinguished between the

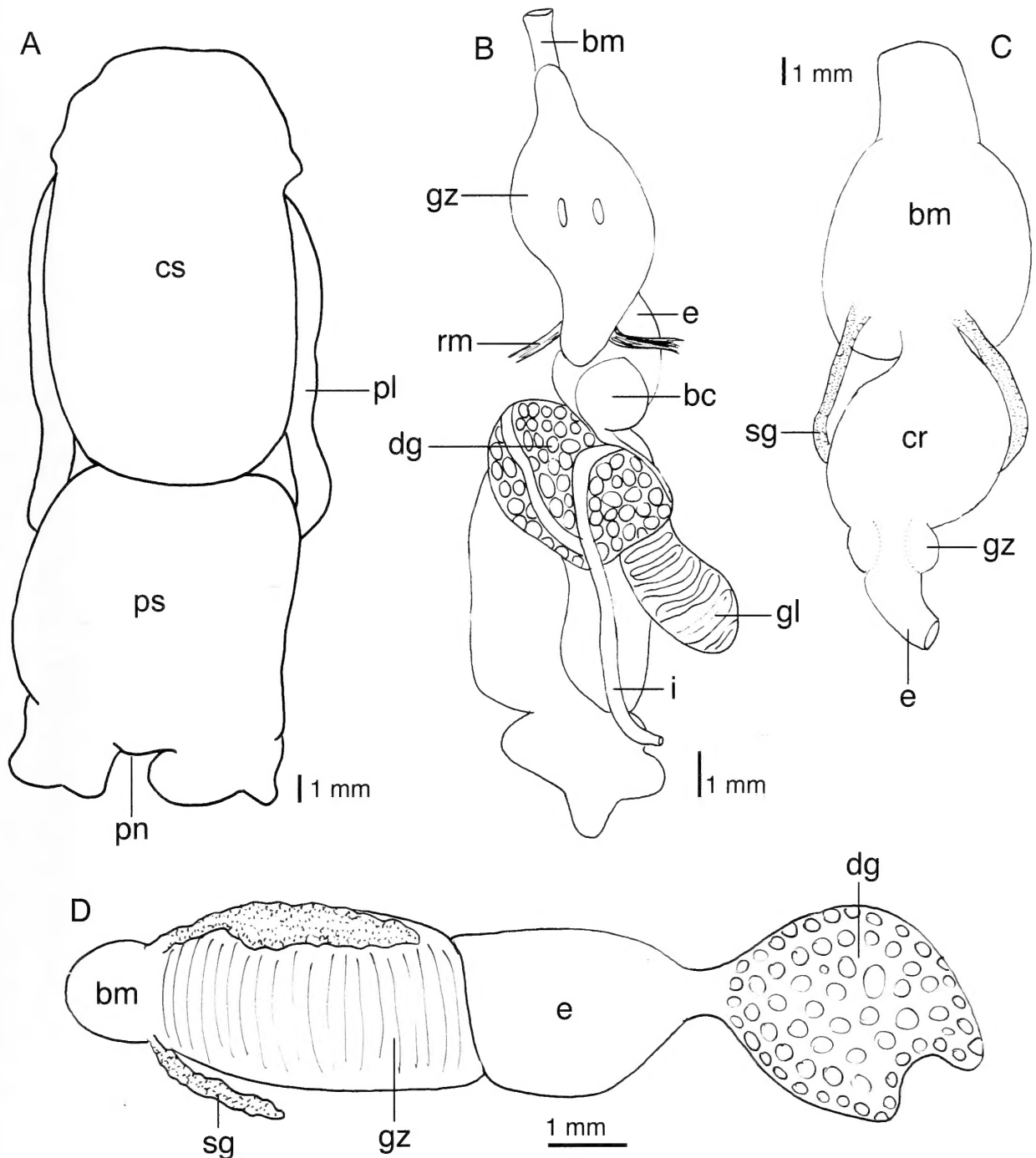


Figure 1. General external morphology and anatomy of species of *Philine* showing the main characteristics of this group and comparing the digestive system of three species. Additional information on the general anatomy can be found in Guiart (1901:107, fig. 59). **A**, dorsal view of a specimen of *P. auriformis* (CASIZ 097499), showing the cephalic shield (cs), posterior shield (ps), parapodial lobes (pl), and posterior notch (pn); **B**, digestive system of *P. puka* (CASIZ 082128), showing that the gizzard plates are typically not covered by muscles (gz); **C**, anterior portion of the digestive system of *P. alba* (CASIZ 076681), showing the small, nonmuscularized gizzard (gz); **D**, digestive system of *P. infundibulum* (CASIZ 076159), showing the muscularized gizzard with the gizzard plates covered with muscles (gz). Abbreviations: bc, bursa copulatrix; bm, buccal mass; cr, crop; cs, cephalic shield; dg, digestive gland; e, esophagus; gl, gill; gz, gizzard; i, intestine; pl, parapodial lobe; pn, posterior notch; ps, posterior shield; rm, retractor muscle; sg, salivary gland.

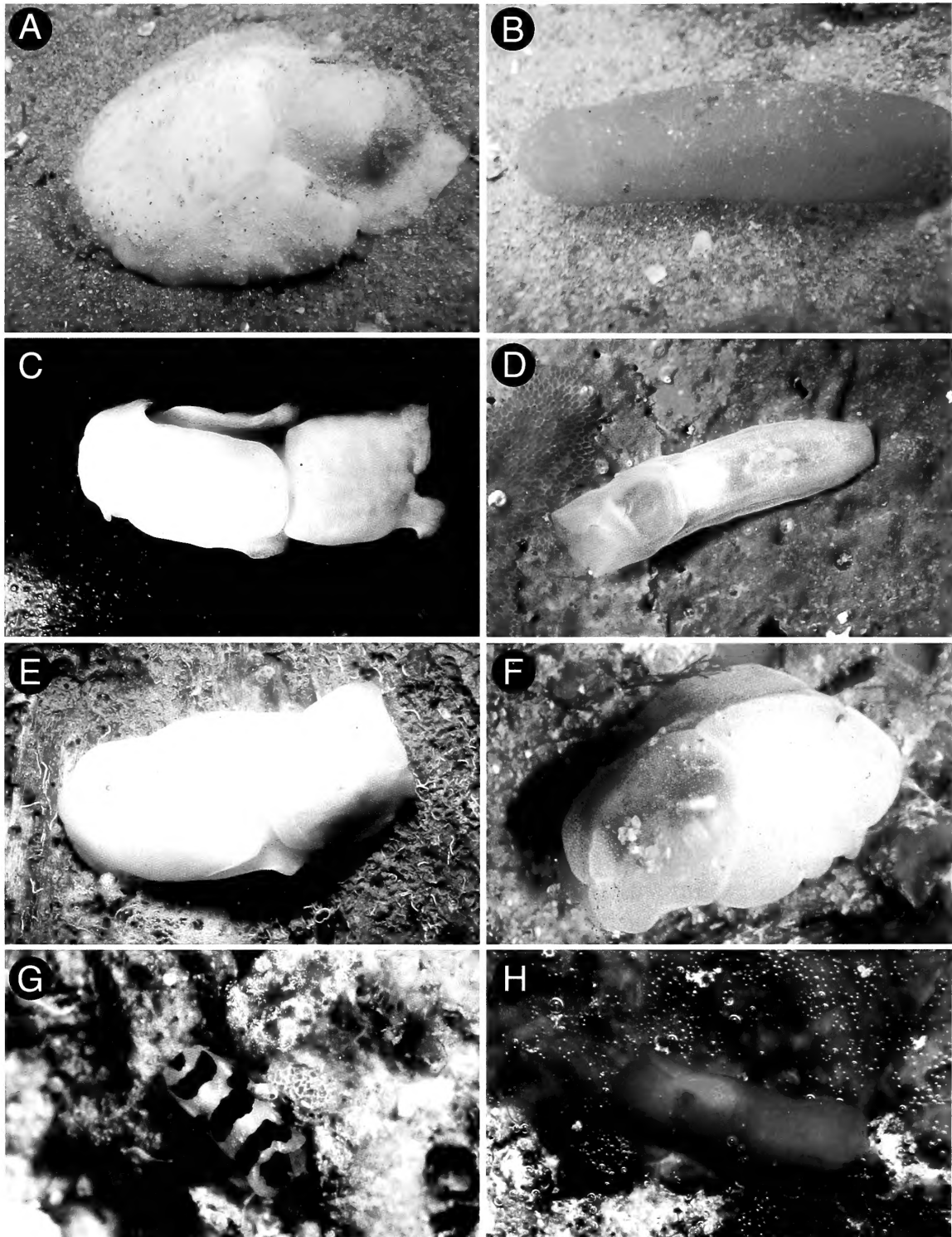


Figure 2. Photographs of living animals: **A**, *P. aperta*, Long Beach, False Bay, Cape Town, South Africa; **B**, *P. aperta*, egg mass, Long Beach, False Bay, Cape Town, South Africa; **C**, *P. auriformis*, Bodega Harbor, California; **D**, *P. elegans*, Mabini, Batangas, Luzon, Philippines; **E**, *P. orientalis*, Matiara Hotel, Langkawi Island, Strait of Malacca, Malay Peninsula, Malaysia; **F**, *P. quadripartita*, Cabo Trafalgar, Spain; **G**, *P. orca*, Madang, Papua New Guinea; **H**, *P. rubrata*, Aldabra Atoll, Seychelles. All photos by T. Gosliner.

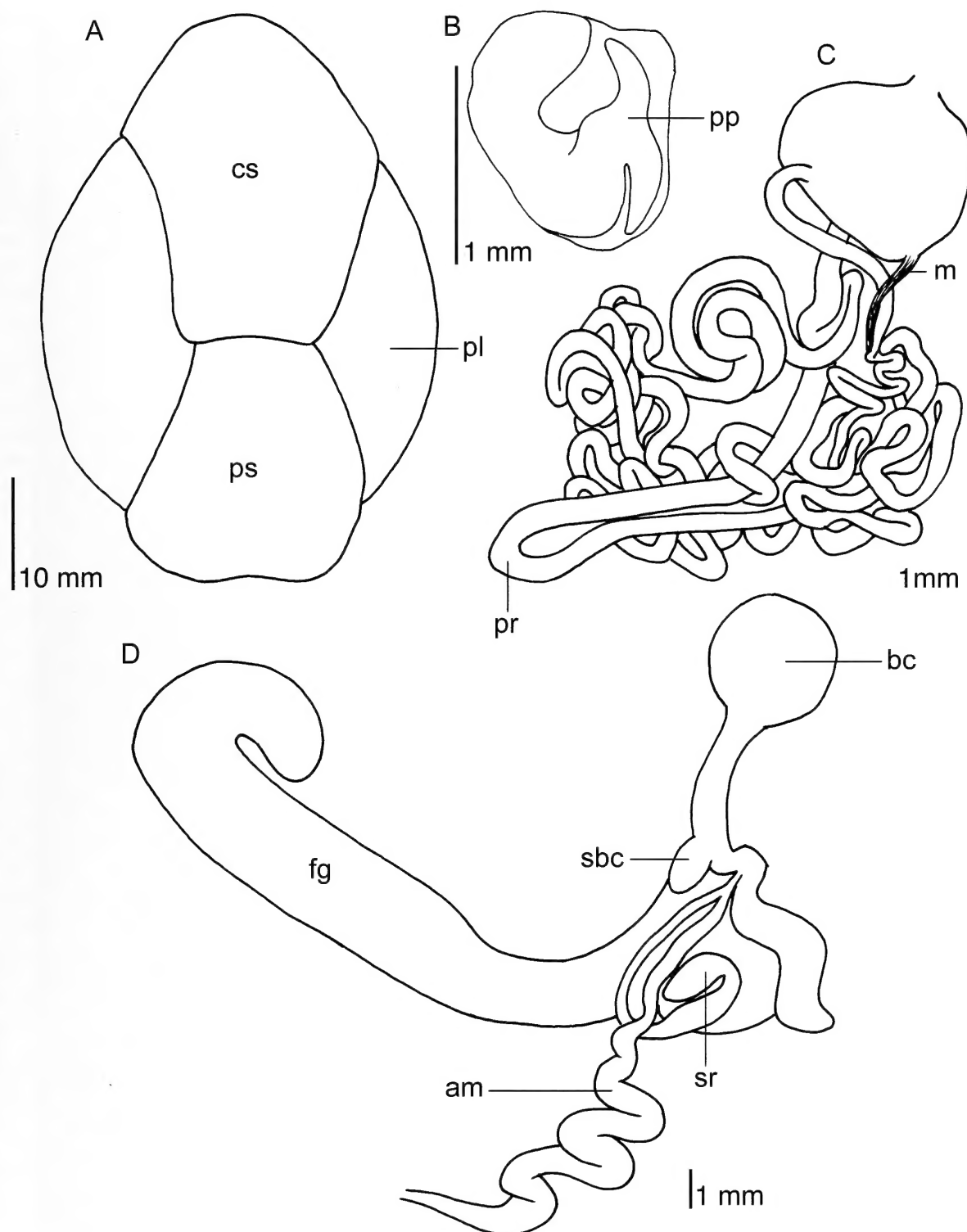


Figure 3. *Philine aperta* (SAM A54288), anatomy: **A**, dorsal view of a living animal; **B**, penis; **C**, male reproductive system; **D**, female reproductive system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **fg**, female glands; **m**, muscle; **pl**, parapodial lobe; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

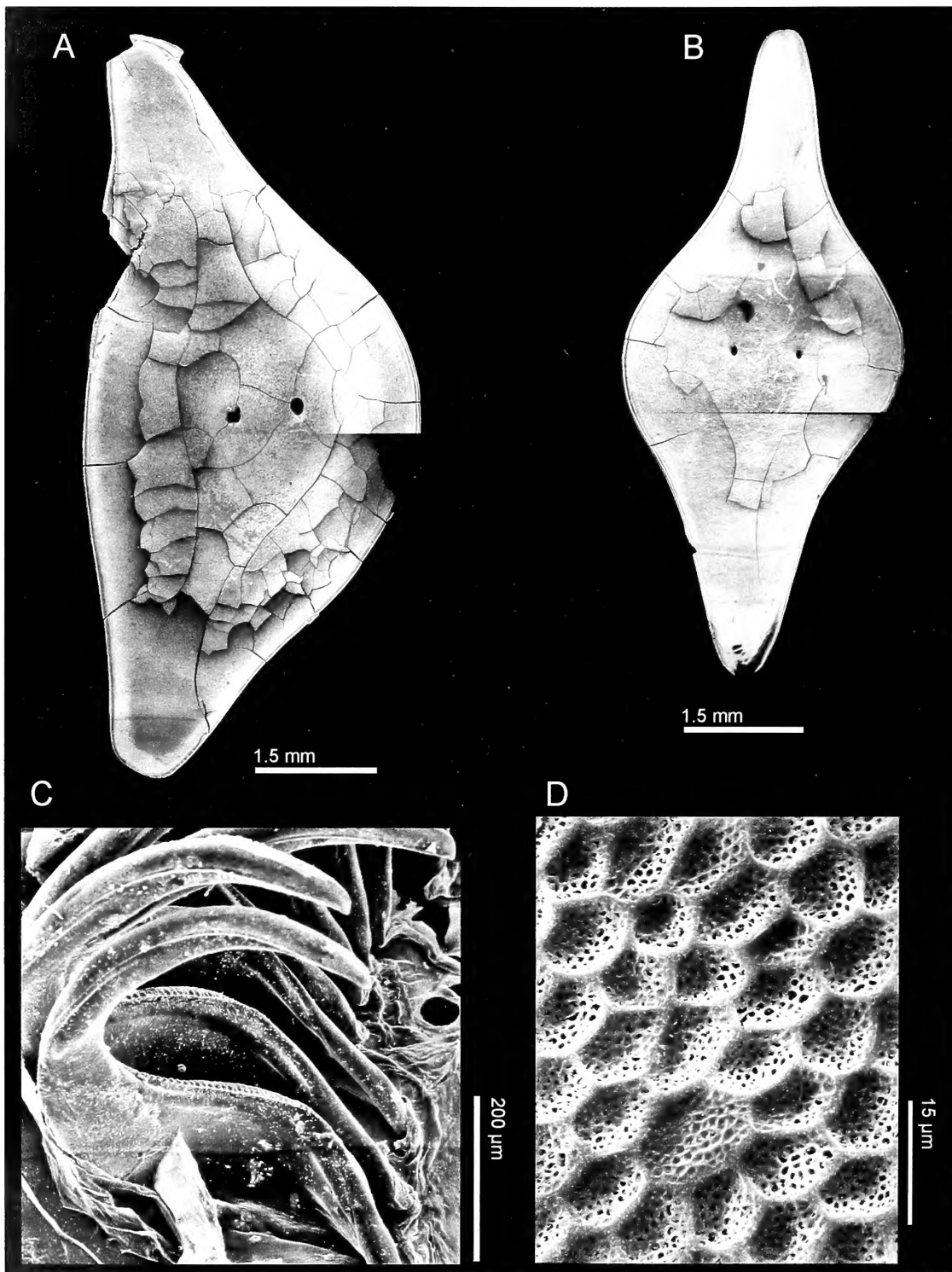


Figure 4. *Philine aperta* (SAM A54288), SEM photographs of internal hard structures: **A**, paired gizzard plate; **B**, unpaired gizzard plate; **C**, radular half-row; **D**, gizzard-plate microsculpture.

two populations by using the broader gizzard plates of *P. aperta* as the basis for separation. They called the members of the European populations *P. aperta aperta*, and they distinguished them from the members of the West African population (*P. a. guineensis*) because of their extremely wide gizzard plates. We agree with their distinction, but based on taxonomic priority, we call the European populations *P. quadripartita* and refer to the South African population *P. a. aperta sensu stricto*. The penial morphology of the Marcuses' *P. a. guineensis* is much more similar to that of *P. aperta* from southern Africa than to that of *P. quadripartita* from Europe because the penial papilla is contained within a penial sac that is not distended. It seems that the West African specimens of *P. a. guineensis* are conspecific with *P. aperta* from southern Africa, but more comprehensive study, perhaps including the addition of molecular data, is necessary to make definite conclusions.

We consider the differences between *P. aperta* and *P. quadripartita* significant at the species level. Because the type locality of *P. aperta* is South Africa, the African animals must retain the name *P. aperta* Linnaeus, 1767, and the European population should be called *P. quadripartita* Ascanius, 1772. As Bergh (1901) observed, there are differences in the penial morphology. The penial papilla of *P. quadripartita* protrudes into the base of the penial sac, which is extended over the prostate. The hammer head in *P. quadripartita* is thick, but the handle is shorter than that of *P. aperta*, and it sits at the base of the penial sac. The hammer head of *P. aperta* is at the top of the penial sac, rather than the base, and it is thin, as if it were squashed. The handle has three lobes and is somewhat convoluted; it is too long to fit neatly into the penial sac. The thin muscle that connects the prostate to the penial sac is longer in *P. quadripartita* than in *P. aperta*. The distinct penial morphology of *P. quadripartita* is also evident in figures provided by Guiart (1901) and Brown (1934:fig. 25).

In addition to the morphological differences, the two species have differently shaped egg masses. In *P. aperta* (Figure 2B), the egg mass is composed of tubular, narrow, elongate sacs that are attached to the sand by a mucous thread. In *P. quadripartita* (Guiart, 1901; Picton, 1999), the egg mass is more globular with an elongate mucous thread that is almost the same length as the globular portion. Molecular systematic studies would further clarify species boundaries and geographical isolation of populations.

Philine alba Mattox 1958

(Figures 5, 6)

Philine alba Mattox, 1958:98, pls. 33, 34.

Material: CASIZ 076681, one specimen, dissected,

southern California, collected by Robert Beeman. CASIZ 101369, 15 specimens, two dissected, off Point Sur, Monterey Bay, California, 36°21.5–20.7'N, 122°0.27–0.60'W, May 10, 1994, M. Eric. Anderson on R/V *Cayuse*. CASIZ 105161, one specimen, dissected, from 445 m depth, off Darwin Island, Galápagos Islands, November 21, 1995, John E. McCosker et al., aboard *Johnson Sea Link*. LACM 63-52, two specimens dissected, more than 10 specimens still intact, 183 m, off Point Pinos, Monterey Co., California (36°38'N, 122°02'W), November 26, 1963, collected by James H. McLean. LACM 172458 two specimens, shell only, 140 m, Santa Monica Bay, California.

Distribution: The type material is from Santa Catalina Island, California (Mattox, 1958), and this species has been found from the Monterey Bay to the Gulf of California. We report the first occurrence from deep water off of the Galápagos Islands.

External morphology: The living animal is uniformly white to yellowish (Behrens & Hermosillo, 2005) with thin parapodial lobes and a long cephalic shield. The posterior shield lacks a posterior notch (Figure 5A). Individuals can reach 6 cm in length.

Internal morphology: The whorls of the shell have a high rate of expansion, and the surface lacks sculpture (Figure 6A).

This species has one short ventral oral gland and one short dorsal oral gland. The buccal mass is large (Figure 5B). The radular formula is 14–24 × 2.1.0/1.1.2 (Mattox, 1958; present study). The inner lateral teeth have zero to seven small denticles, and vestigial rachidian teeth may be present (Figure 6E). There is a distinct gizzard, although it is not muscularized. Three small, equally sized, and kidney-shaped gizzard plates rest in the bottom of the gizzard (Figure 6B, C). The gizzard plates have indistinct microsculpture (Figure 6D). The esophagus widens posteriorly. Prominent salivary glands span the esophagus from the posterior tip of the buccal mass to the anterior tip of the crop (Figure 5B).

The parietal and pleural ganglia are fused. The genital ganglion is distinct, although minute and difficult to see. Halfway between the parietal-pleural ganglion and the visceral ganglion is the supaintestinal ganglion, and the osphradial nerve branches from it (Figure 5C). The subintestinal ganglion is adjacent to the visceral ganglion.

The penial sac is large and round with a smooth sheath and two conical papillae that lack armature (Figure 5D). The simple, hook-shaped, single-lobed prostate has no convolutions.

The posterior reproductive system contains a secondary receptaculum and an unbranched hermaphro-

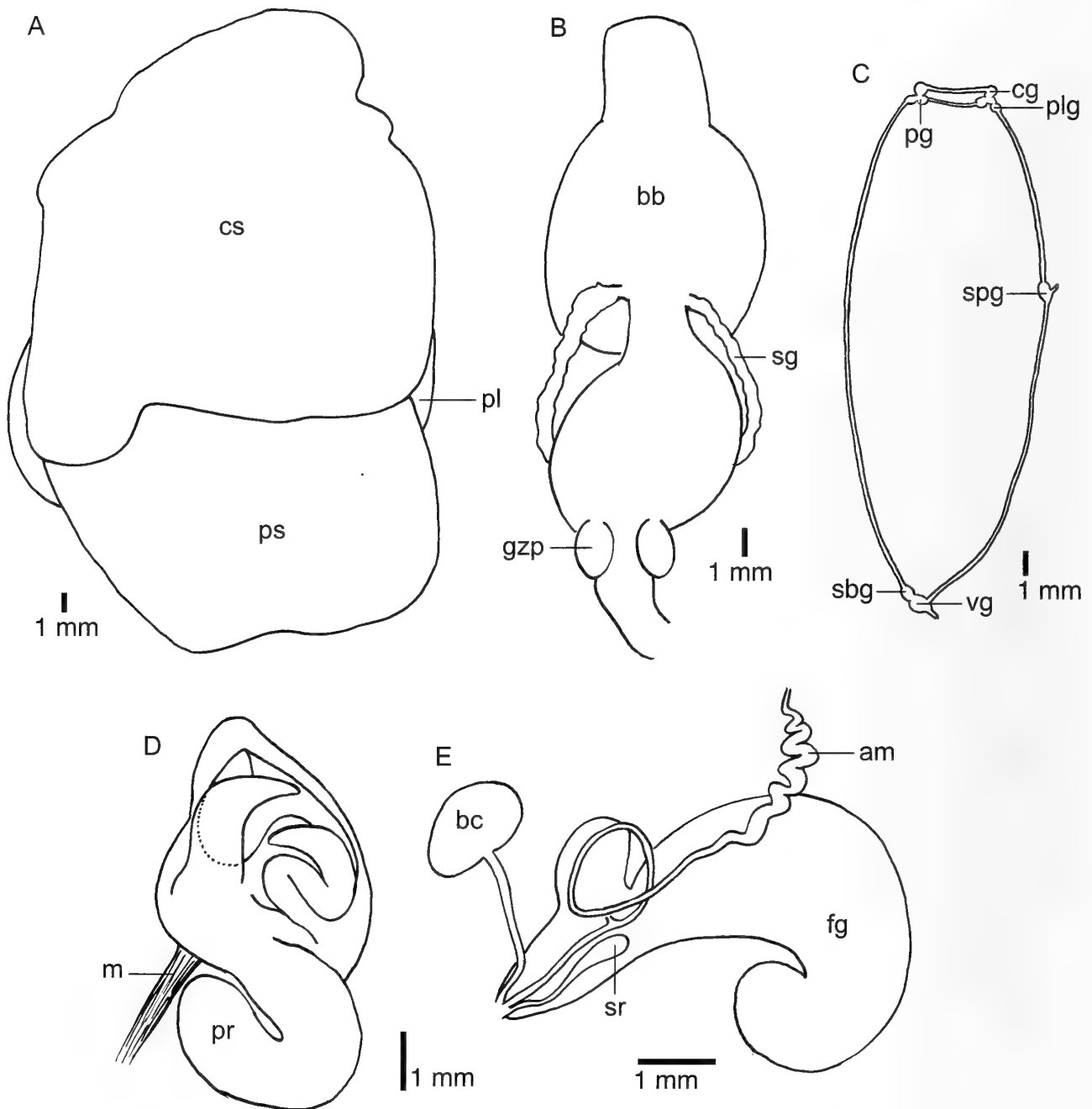


Figure 5. *Philine alba* (CASIZ 076681), anatomy: **A**, dorsal view of a living animal; **B**, anterior portion of the digestive system; **C**, nervous system; **D**, male reproductive system; **E**, female reproductive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **gzp**, gizzard plate; **m**, muscle; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **sg**, salivary gland; **spg**, suprainintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

ditic duct (Figure 5E). The ampulla is convoluted, and there is a single receptaculum seminis located at the base of the genital aperture. The mucous gland is large and free at the distal end. There is a single bursa copulatrix.

Discussion: *Philine alba* is not part of the *P. aperta* clade (see Phylogenetic Analysis and Figures 38, 39). Our specimens closely match Mattox's original description (1958), allowing us to enhance his discussion with figures of the whole animal, radula, and gizzard

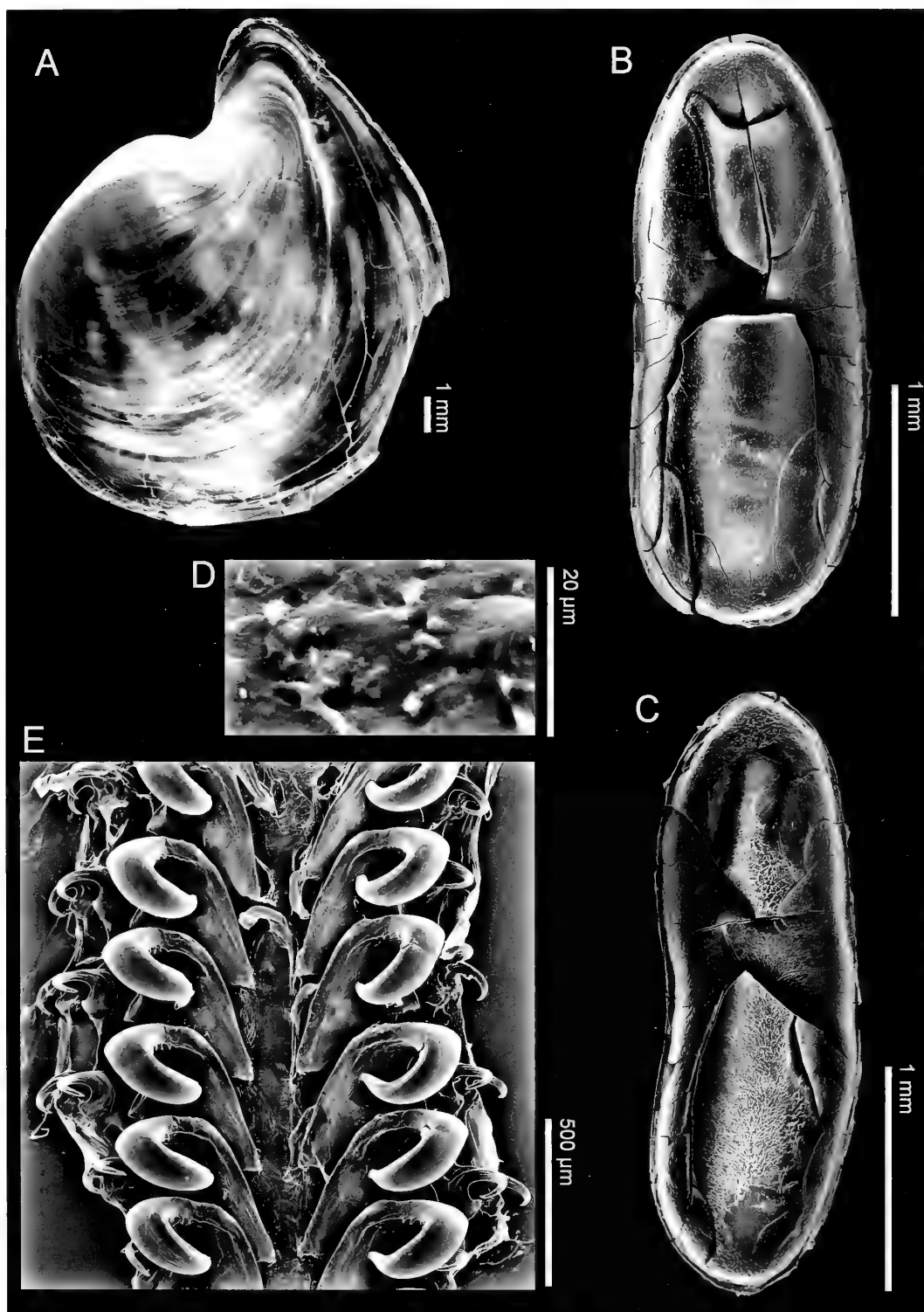


Figure 6. *Philine alba* (CASIZ 076681), micrographs of internal hard structures: **A**, light micrograph of the ventral side of the shell; **B**, **C**, SEM photographs of the gizzard plates; **D**, SEM photograph of the gizzard-plate microsculpture; **E**, SEM photograph of the radular teeth.

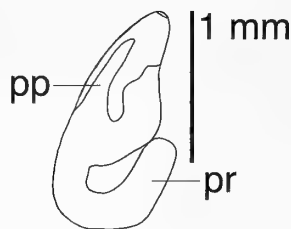


Figure 7. *Philine alboides* (USNM 897330), male reproductive system. Abbreviations: **pp**, penial papilla; **pr**, prostate.

plates. Mattox reported no rachidian teeth, but we found some that are highly reduced and probably vestigial (Figure 6E).

The specimens from California to the Galápagos Islands of the eastern Pacific differ from those that Marcus (1974) described as having a distribution from the western Atlantic of Florida to Rio de Janeiro. Marcus (1974:fig. 103) reported that the penis of her specimens had “a folded atrium and no true penial papilla,” but our specimens (Figure 5D) and Mattox’s had multilobed papillae (Mattox, 1958). Furthermore, the gizzard plates in Mattox’s specimens are small ovals with a convex inner surface, whereas in Marcus’s specimens they are pointed on the inner surface, reminiscent of the gizzard plates of members of the genus *Scaphander*. In all likelihood, Marcus’s specimens represent a distinct species. Additional material from the Atlantic is compared to confirm these apparent distinctions, but the two seem to be distinct species from different ocean basins.

Philine alboides Price, Gosliner, and Valdés, sp. nov.

(Figures 7, 8)

Philine alba Mattox, 1958; Marcus and Marcus, 1967:607, figs. 23–28; Marcus, 1974:359, figs. 102, 103, misidentification.

Material: Holotype: USNM 836707, Station 199, R/V *Pillsbury*, 311–329 m depth, off the east coast of Florida, between 27°59’N, 79°20’W and 27°30’N, 79°10’W, August 11, 1964. Paratypes: USNM 897330, one specimen, 329 m depth, off Louisiana, Gulf of Mexico, 28°04’N, 90°17’W, November 6, 1963, R/V *Gyre*. USNM 836704, R/V *Pillsbury*, Station 446, one specimen, dissected, 110–298 m depth, Gulf of Mosquitos, Panama, 8°58’6”N, 81°26’18”W, July 21, 1966.

Distribution: Known from the Straits of Florida, the Gulf of Mexico (Louisiana; present study) and the Caribbean to Rio de Janeiro, Brazil (Marcus & Marcus, 1967; Marcus, 1974).

Etymology: The name *alboides* is a noun in apposition and comes from the Latin meaning ‘like alba.’ It refers to the fact that this species has previously been confused with *P. alba*. Type locality: Straits of Florida, USA.

External morphology: The preserved animal is uniformly white, 19–44 mm in length with thin parapodial lobes and a long cephalic shield. The posterior shield lacks a posterior notch.

Internal morphology: The whorls of the shell have a high rate of expansion, and the surface lacks sculpture. Because the shell is fragmented, we left it in the animal and could not take a scanning electron image. Its shape is open and broad as in *P. alba*.

This species has one short ventral oral gland and one short dorsal oral gland. The buccal mass is large. The radular formula is $16 \times 2.1.0.1.2$ in the holotype. The inner lateral teeth lack any trace of denticles, and vestigial rachidian teeth are absent (Figure 8A). There is a distinct gizzard, although it is not muscularized. Only one gizzard plate (Figure 8B) was found in the partially dissected holotype specimen, but all three plates were contained in a vial in one paratype (USNM 836704). The plates are ovoid at the base and sharply angled with a high, rounded apex. The esophagus widens posteriorly. Prominent salivary glands span the esophagus from the posterior tip of the buccal mass to the anterior tip of the crop.

The parietal and pleural ganglia are fused. The subintestinal ganglia and visceral ganglia are adjacent to each other; a distinct genital ganglion was not evident and is presumably fused to the visceral ganglion. Halfway between the parietal-pleural ganglion and the visceral ganglion is the suprainintestinal ganglion, and the osphradial nerve branches from it. The penial sac is large and round with a smooth, conical papilla that lacks armor (Figure 7). The relatively short prostate curves anteriorly. The posterior reproductive organs were examined in one paratype (USNM 836704).

The ampulla is highly convoluted, and it curves around the smaller albumen and membrane glands. A proximal receptaculum was not evident but that may be because the specimen was not particularly well preserved. The hermaphroditic duct branches to the albumen and membrane glands and continues as an elongate tube. Immediately before its junction with the genital aperture, it is joined by a distal receptaculum seminis. The duct of the large, rounded bursa copulatrix is moderately long and joins the bulbous genital atrium, where a single bursa copulatrix also is situated.

Discussion: Although *P. alboides* is not part of the *P. aperta* clade (see Phylogenetic Analysis), we recognized

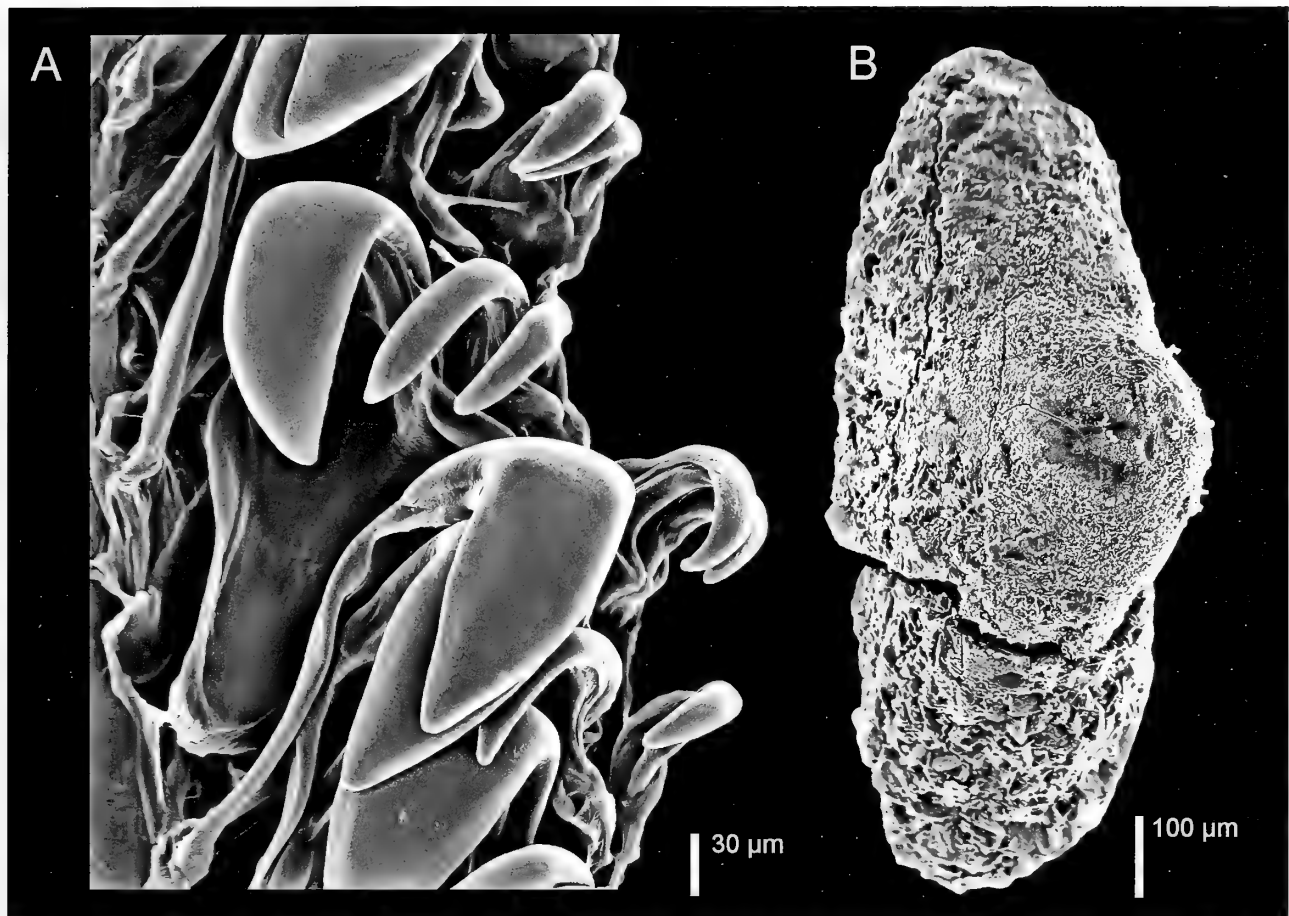


Figure 8. *Philine alboides* (USNM 897330), SEM photographs of internal hard structures: **A**, Radular teeth; **B**, gizzard plate.

the distinction between this species and *P. alba* while undertaking this study.

Our specimens closely match the descriptions in Marcus & Marcus (1967) and Marcus (1974) of *P. alba*, and their illustrations are, with the exception of the anatomy of the penial papilla (illustrated herein in Figure 7), sufficient for identifying this species. The present material and the Marcuses' descriptions have several consistent morphological differences with that of *P. alba*, which is known only from the eastern Pacific. *Philine alboides* has a radula with inner lateral teeth lacking denticles, whereas *P. alba* always has small denticles. The gizzard plates of *P. alboides* are more rounded and higher in profile than the ovoid, more flattened plates of *P. alba*. The penis of *P. alboides* has a recurved simple prostate whose distal end faces anteriorly (Marcus & Marcus, 1967; Marcus, 1974; present study), whereas that of *P. alba* is directed posteriorly. In addition, the penial papilla of *P. alboides* has a single primary papilla, whereas in *P. alba* two distinct papillae are present. Based on the consistency of these differences and the fact that the two taxa are

separated by the Isthmus of Panama, we consider the Atlantic material to represent a distinct species, which we call *P. alboides*. Both *P. alba* and *P. alboides* are unique among described *Philine* species in having a distal receptaculum seminis situated near the genital atrium.

Philine angasi (Crosse & Fischer, 1865)

(Figures 9, 10)

Bullaea angasi Crosse and Fischer, 1865:38, pl. 2.

Philine angasi (Crosse and Fisher), Rudman, 1970:30, figs. 1A, F–H, pl. 3G; Rudman, 1972b:460, figs. 1–4.

Material: BMNH 1996408, 12 specimens (3 dissected), Port Jackson, Sydney, New South Wales, Australia, collected by I. Bennett.

Distribution: Known from northern New Zealand and from southern Australia in portions of New South Wales, Victoria, Tasmania, South Australia, and southern Western Australia (Rudman, 1970).

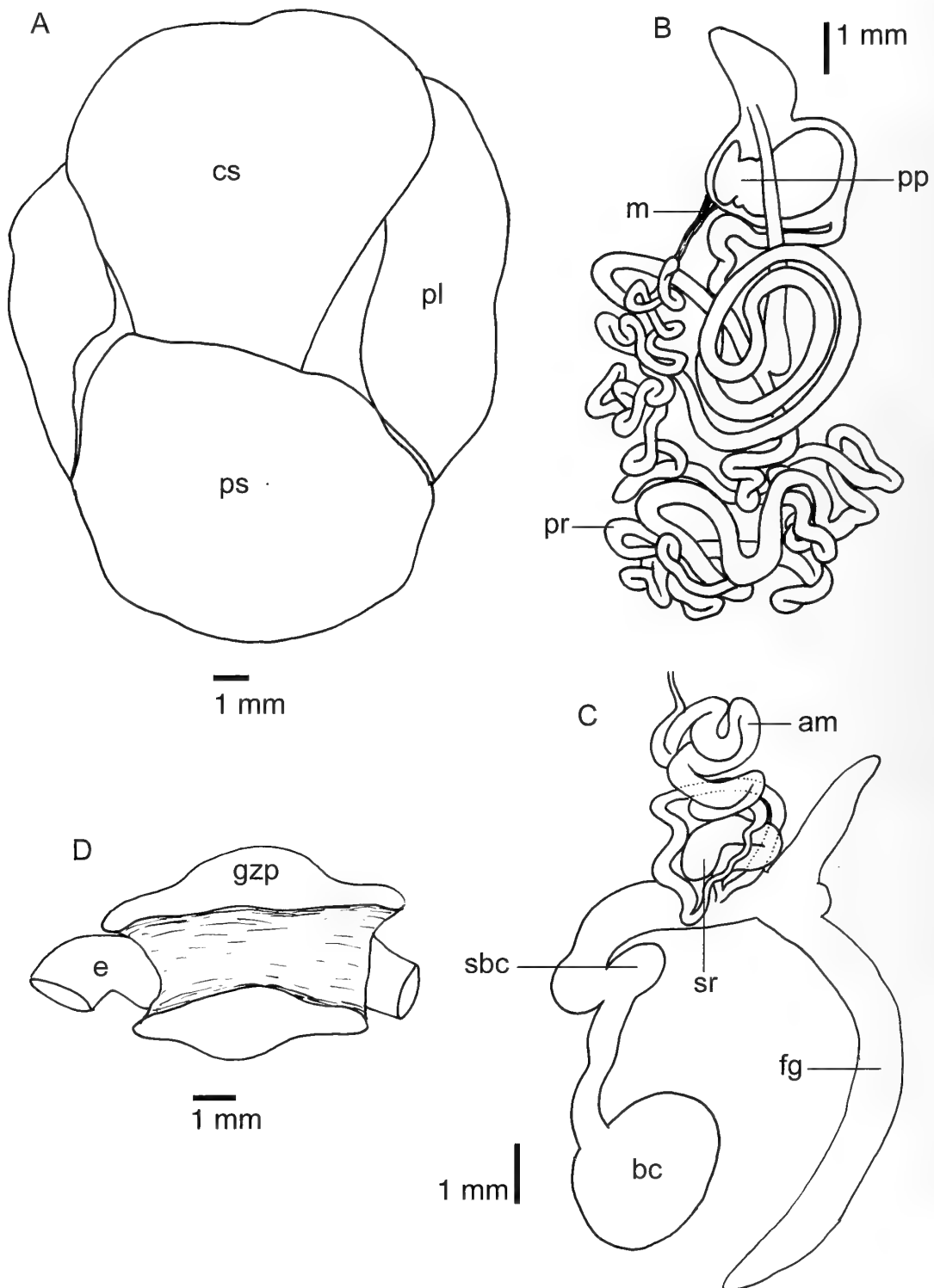


Figure 9. *Philine angasi* (BMNH 1996408), anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, female reproductive system; **D**, gizzard. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **e**, esophagus; **fg**, female glands; **gzp**, gizzard plate; **m**, muscle; **pl**, parapodial lobe; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

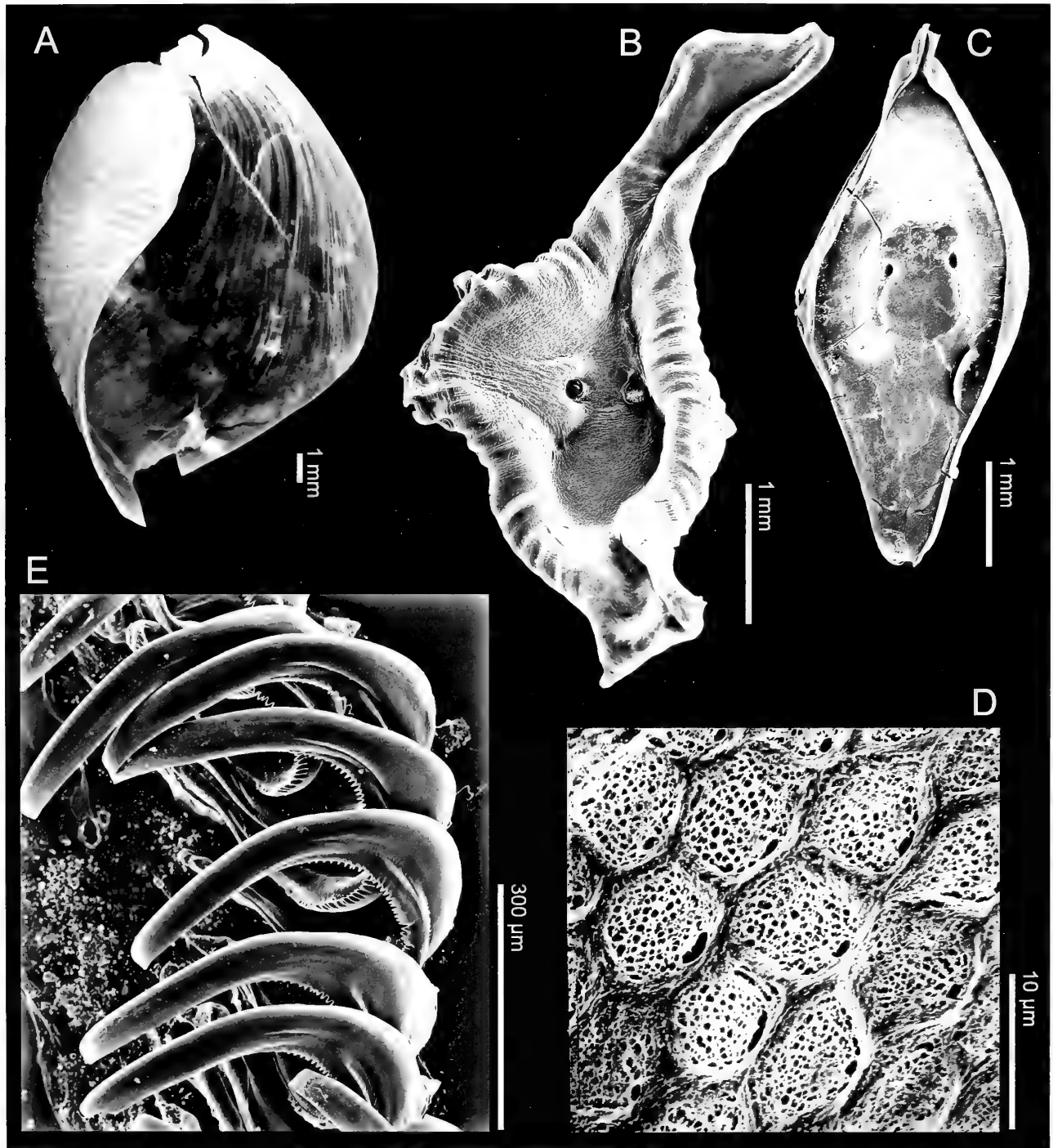


Figure 10. *Philine angasi* (BMNH 1996408), micrographs of internal hard structures: **A**, light micrograph of the ventral side of the shell; **B**, SEM photograph of a paired gizzard plate; **C**, SEM photograph of the unpaired gizzard plate; **D**, SEM photograph of the gizzard-plate microsculpture; **E**, SEM photograph of the radular teeth.

External morphology: The preserved animals are uniformly white (Rudman, 1998b) and reach 10 cm in length. The cephalic shield is longer than the posterior shield, and the parapodial lobes are thin (Figure 9A).

The posterior shield does not have a notch in the preserved specimens, but the photograph of the living animal (Rudman, 1998b) clearly shows a well-developed notch.

Internal morphology: The shell is relatively tightly coiled for this clade (Figure 10A), and it has a spine on the last whorl where the outer lip meets the spire. The surface lacks punctuation but is slightly ribbed.

There are two ventral oral glands, but this species lacks dorsal oral glands. The radular formula is $20 \times 1.0.1$. The broad inner lateral teeth have approximately 50–60 small denticles (Figure 10E). The gizzard is muscularized and surrounded by large gizzard plates (Figure 9D); it lacks a distinct crop posterior to the plates. The three spindle-shaped plates have medium-sized pores (Figure 10B, C) and a microsculpture that consists of regularly arranged polygons (Figure 10D). One plate (Figure 10C) is smaller than the two paired plates (e.g., Figure 10B). The salivary glands are short.

The suprainestinal ganglion is located toward the anterior of the visceral loop and is adjacent to or adjoining the fused pleural-parietal ganglion. The subintestinal ganglion is adjacent to the visceral ganglion, but the genital ganglion remains distinct.

The penial papilla is hammer-shaped with subequal lobes and sits directly on a cushion-shaped base that does not distend the wide penial sac (Figure 9B). The convoluted prostate branches to a long, coiled ejaculatory duct that is surrounded by the prostate. A short muscle connects the end of the prostate to the sac.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 9C). The mucous gland is large, and it bends at the free end. There is a single secondary bursa copulatrix.

Discussion: *Philine angasi* is the only species in the *P. aperta* clade that has a spine on the spire side of the last whorl of the shell. The spine is short and stubby.

The paired gizzard plates are similar to those of *P. elegans*, in that they have an S-like twist to their shape. The edges lack the fringes found in *P. elegans*, but they are crenulated. The unpaired plate is symmetrical and more oblong than the homologous plate in *P. elegans*. The microstructure of the gizzard plate consists of a mesh of regularly shaped polygons, as in *P. aperta* and *P. puka*.

The penial morphology of *P. angasi* is most similar to that of *P. orientalis*. These papillae are relatively small and columnar, although *P. angasi* lacks an additional lobe on the base of the papilla that is present in *P. orientalis*.

Philine auriformis Suter, 1909

(Figures 2C, 11, 12)

Philine auriformis Suter, 1909:157. Rudman, 1970: 24, fig. 1b–e, 2P, pl. 3, figs. d–f, h, o; Gosliner, 1995:122, figs. 1–3.

Material: CASIZ 097499, approximately 100 specimens, 10–35 mm preserved length, three dissected, trawled in 4 m depth, between Dumbarton and San Mateo Bridges on western side of San Francisco Bay, California, July 30, 1993, T. Gosliner et al.

Distribution: *Philine auriformis* is originally from New Zealand (Rudman, 1970, 1972a, b). It has been introduced to the western coast of North America and can now be found from San Diego to Bodega Bay (Gosliner, 1995).

External morphology: The living animal (Figure 2C) is uniformly white, varying in length from 1 to 4 cm. The broad cephalic shield is longer than the posterior shield (Figure 11A). The posterior shield is notched, and the parapodial lobes are flimsy.

Internal morphology: The whorls of the shell have a high rate of expansion, and the perimeter of the shell is ovate (Figure 12). The sculpture is punctate.

There is a single, short ventral oral gland and two dorsal oral glands. The radula has the formula $21 \times 1.1.0.1.1$. The broad inner lateral teeth have 30 to 50 denticles. The crop is indistinct, and the gizzard is muscularized. The gizzard plates, however, are not covered with muscles, and the esophagus passes between them. The three spindle-shaped plates have approximately the same size and shape. Each plate has two long indentations on the dorsal side.

The fused pleural-parietal ganglion is adjacent to or adjoining the anterior suprainestinal ganglion. The osphradial nerve may branch from the suprainestinal ganglion or from halfway between the suprainestinal and visceral ganglia. The genital ganglion is fused to the visceral ganglion and is adjacent to the subintestinal ganglion.

The small penial papilla is hammer-shaped (Figure 11C). The penial sac is pyriform (Figure 11B). The lobes of the hammer head are subequal, the smaller of which looks like a little knob above the papilla stalk. The convoluted prostate branches, and a short muscle connects it to the end of the penial sac. The ejaculatory duct is short and completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes, and the free end bends over. There is a knob at the wide base of the spherical, thin-walled bursa copulatrix.

Discussion: Gosliner (1995) observed that this species, originally described from New Zealand, was introduced to the California coast. Rudman (1998a) disagreed with the identification, claiming that the ejaculatory duct in the California specimens was much smaller than specimens from New Zealand and that the size of the

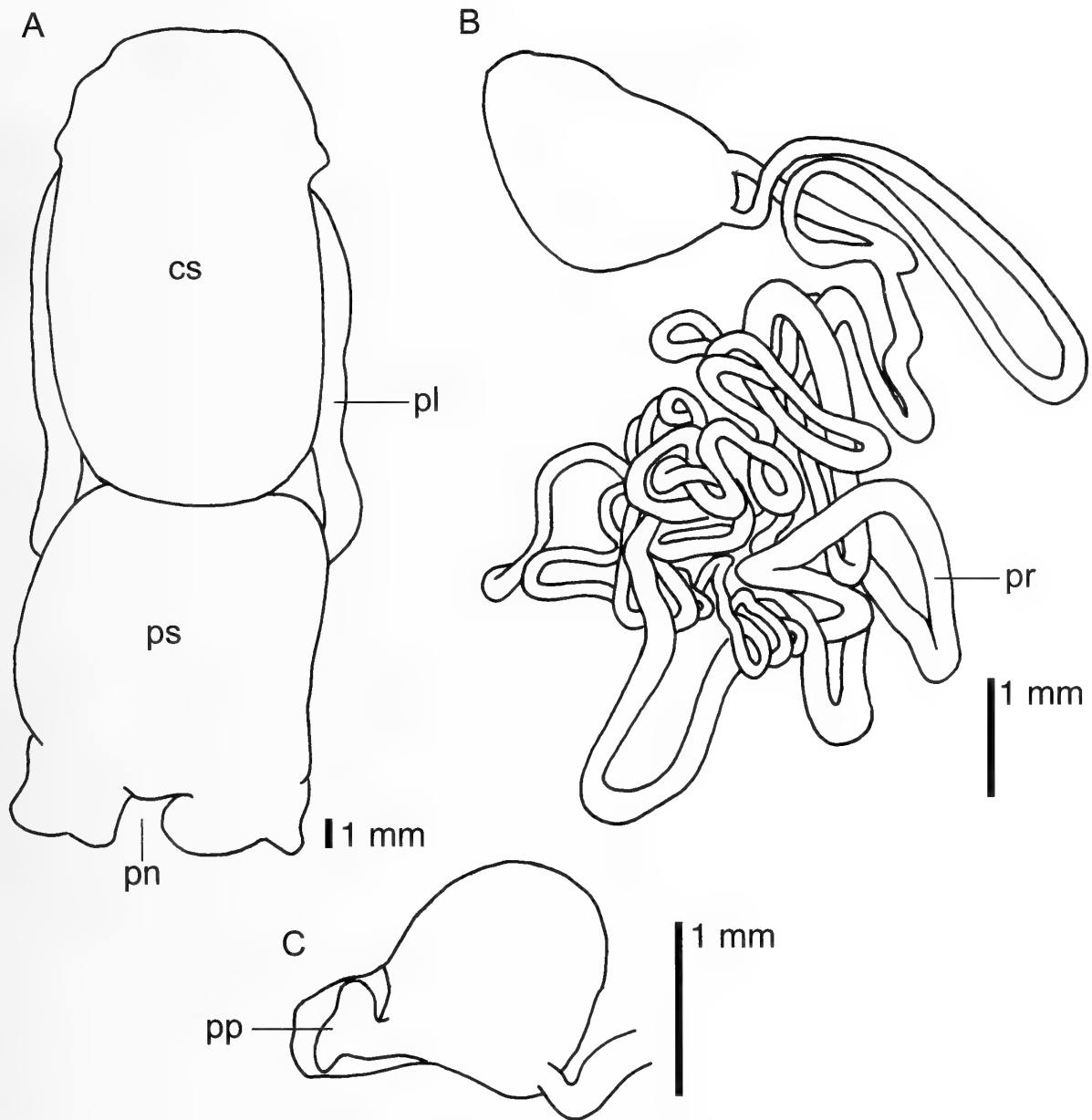


Figure 11. *Philine auriformis* (CASIZ 097499), anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, penis. Abbreviations: **cs**, cephalic shield; **pl**, parapodial lobe; **pn**, posterior notch; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield.

entire radula differed and was much smaller in the New Zealand specimens. However, Rudman illustrates considerable variation in the degree of elaboration of the ejaculatory duct on his website. The ejaculatory duct illustrated in Gosliner's article is intermediate between the extremes that Rudman illustrates from New Zealand and California. The specimen from California illustrated here (Figures 11, 12) is much more similar to Rudman's specimen from New Zealand than it is to the specimen he illustrated from California. Given this variation, there is no reason to suggest that

these represent different species, especially because *P. auriformis* is the only large species with this type of distinctive gizzard-plate morphology. The only other species with similar gizzard plates is *Philine fenestra*, described here. Also, *P. auriformis* is the only species found near shallow-water harbors that would probably be introduced through ballast water discharge (Gosliner, 1995).

The three equal-sized gizzard plates and the punctate shell suggest this species is plesiomorphic in the *P. aperta* clade. *Philine fenestra*, *Philine finmarchica*, and

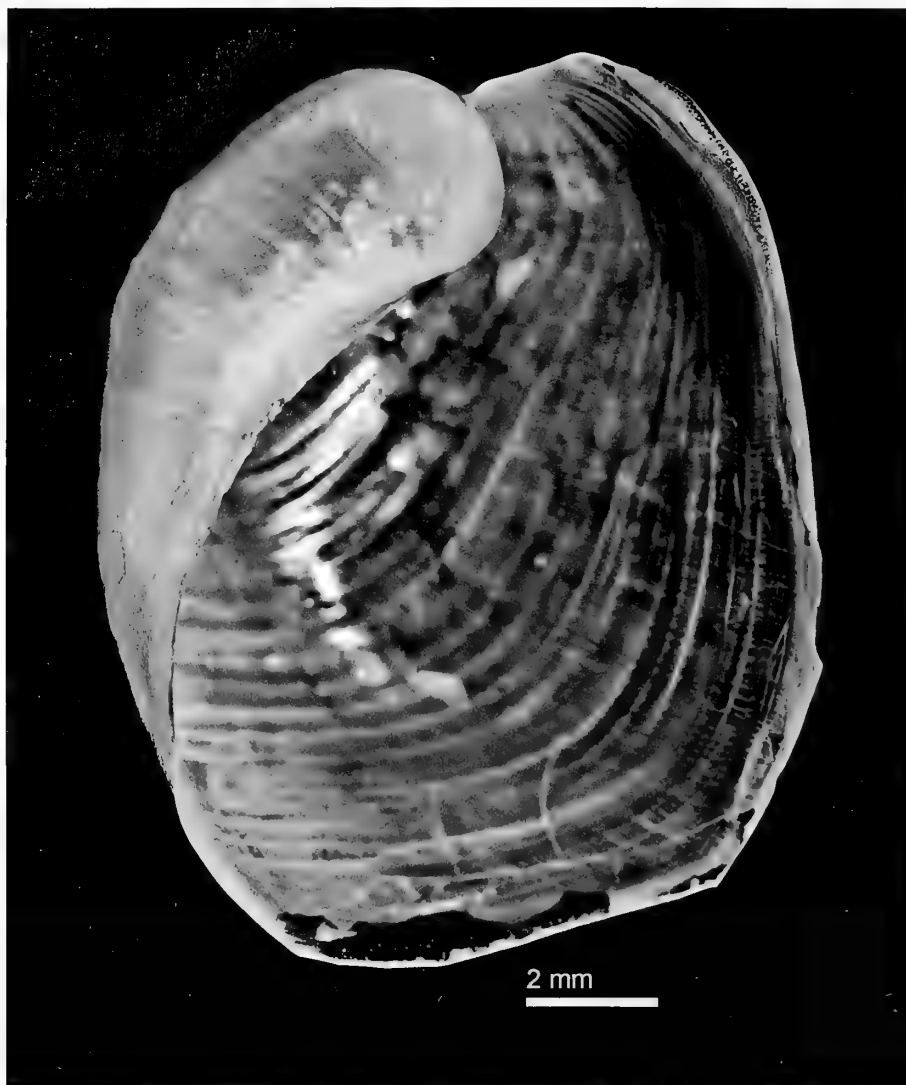


Figure 12. *Philine auriformis* (CASIZ 097500). Light micrograph of the ventral side of the shell.

Philine thurmanni thurmanni are the only other members of this clade that have equal-sized plates. The penial papilla of *P. auriformis* is hammer-shaped, although the hammer is much smaller than in other members of the clade; the lobes barely protrude over the base of the papilla. The slits on the gizzard plates are shallower and shorter than those found on the plates of *P. fenestra*. The shell and posterior reproductive system has been illustrated previously (Gosliner, 1995), although we have provided additional detail regarding the penial morphology.

Philine babai Valdés, 2008

(Figure 13)

Philine babai Valdés, 2008:721–722, figs. 64C–E, 67.

Material: MNHN (no specimen number), one dissected specimen, Station DW08, 435 m, New Caledonia, 20°134'S, 164°54'W.

Distribution: *Philine babai* is known from Indonesia, Fiji, New Caledonia, Tonga, and Wallis Island from 230 to 533 m.

External morphology: The preserved animals are uniformly white and approximately 2 cm in length. The cephalic shield is longer than the posterior shield. The posterior shield lacks a posterior notch. The parapodial lobes are narrow.

Internal morphology: The whorls of the shell are tightly coiled for this clade, and the shell is punctate.

There are no ventral or dorsal oral glands. The

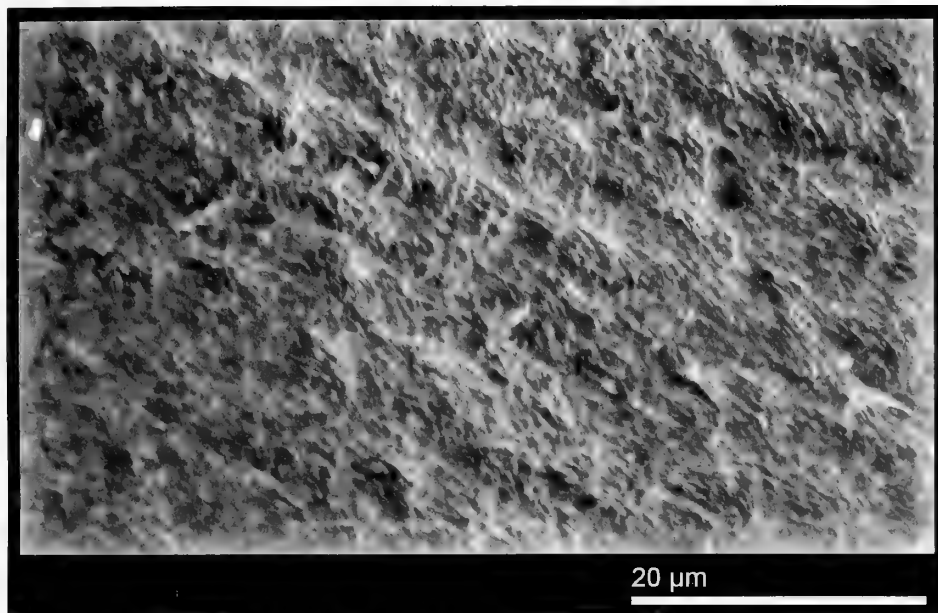


Figure 13. SEM photograph of the gizzard-plate microsculpture of *P. babai* (MNHN no specimen number).

buccal bulb is small, and the radular formula is $16 \times 1.0.1$ with 35 small denticles on the inner side of the broad inner lateral teeth. The crop is indistinct. The gizzard is muscularized, but the three plates are not covered with muscles. The plates are roughly spindle-shaped. The central plate is broad with a ruffled edge, smaller than the other two, and has two small slits, one on each edge of the outer side of the plate. The paired plates are mirror images of each other, and they have an S-like twist, and two long slits on the sides. The slit on the inner edge is longer than the slit on the outer edge. The microsculpture of the gizzard plates lacks structure (Figure 13). The salivary glands are short.

The fused pleural-parietal ganglion adjoins the anterior suprainestinal ganglion. The osphradial nerve branches may branch from the suprainestinal ganglion or from halfway between the suprainestinal and visceral ganglia. The genital ganglion remains distinct from the visceral ganglion but is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has subequal lobes and distends the base of the pyriform penial sac over the convoluted prostate. The papilla rests directly on the base of the penis, and is not supported by a stalk. The ejaculatory duct branches from the convoluted prostate, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is long.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches a single, long, and narrow receptaculum seminis (Figure 14). The female gland is relatively small for this clade. The

bursa copulatrix is large with a single secondary bursa copulatrix.

Discussion: *Philine babai* (Valdés, 2008), *P. auriformis*, *P. fenestra*, *Philine infundibulum*, and *Philine sarcophaga* all have slits on their gizzard plates, although *P. sarcophaga* and *P. infundibulum* lack slits on their unpaired plates. The plates of *P. auriformis* and *P. fenestra* are all the same size and shape, which makes *P. babai* the only species with slits also present on its wide, unpaired plate. The slits on the unpaired plate of *P. babai* however are very reduced. This unpaired plate has ruffled edges; these ruffles are much broader than the crenulations edging the paired plates in *P. angasi*. The unpaired plate is rhomboidal, as are the unpaired plate of *P. elegans*, *P. infundibulum*, and *P. sarcophaga*. The gizzard plates lack any discernible microsculpture.

The reduced penial papilla in *P. babai* (Valdés, 2008) is similar to that in *P. auriformis*. The tip of the papilla has slightly unequal lobes, and the papilla rests on a fat base.

Philine elegans Bergh, 1905

(Figure 2D, 15, 16)

Philine elegans Bergh, 1905:31, pl. 9, figs. 9–13.

Material: CASIZ 083758, one specimen, dissected, Anilao, Mabini, west side of Calumpan Peninsula, Batangas Province, Luzon Island, Philippines, collected February 23, 1992 by T. M. Gosliner. California

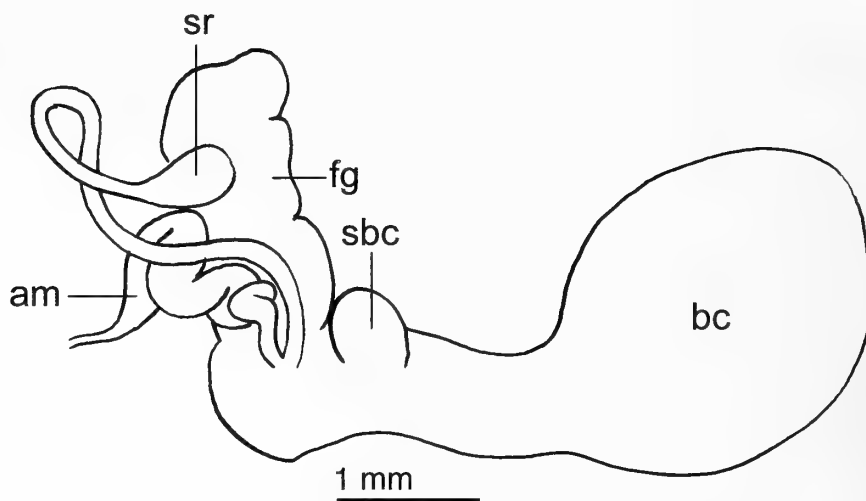


Figure 14. Female reproductive organs of *P. babai* (MNHN no specimen number). Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **fg**, female glands; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

Academy of Sciences, San Francisco, CASIZ 086710, two specimens, one partially dissected, Wair Mitak, Flores, Indonesia, collected April 25, 1992 by P. Fiene.

Distribution: Specimens have been found from Saleh Bay, Subawa Island (type locality), and Flores Island, Indonesia (Bergh, 1905; present study) and Luzon Island, Philippines (present study).

External morphology: The living animal (Figure 2D) is uniformly white and approximately 1 cm in length. The cephalic shield is longer than the posterior shield (Figure 15A). The parapodial lobes are thin, and the posterior notch is deep.

Internal morphology: The shell was not preserved in the material we studied, so we concluded from an apical drawing in Bergh (1905) that the whorls of the shell have a high rate of expansion. The surface of the shell is smooth.

There are two short, closely appressed dorsal oral glands and one short ventral oral gland. The buccal bulb (Figure 15B) and radula are reduced; the radular formula is $21 \times 1.0.1$. The inner lateral tooth is broad with 33 denticles on the oldest tooth and 51 on the youngest (Figure 16D). The crop is indistinct. The gizzard is muscularized, but the large plates are not covered with muscles. The gizzard plates are delicately fringed around the margin (Figure 16A, B). The fringes are irregularly spaced around the margin of the plate. The unpaired plate is small and either diamond-shaped or oval (Figure 16A). The other two plates are approximately the same size and shape. These two plates are roughly spindle-shaped with an S-like twist (Figure 16B). All three plates have pores. The microsculpture is made of deep, regular impressions that are

larger than the impressions found in other species (Figure 16C). The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior suprainestinal ganglion (Figure 15B). The osphradial nerve branches from the right lateral nerve midway between the suprainestinal and visceral ganglia. The genital ganglion is fused to the visceral ganglion and is adjacent to the subintestinal ganglion.

The penial sac is ovate (Figure 15C). The base of the penial papilla is a round cushion. A short stalk leads up to the hammer-shaped penial papilla. The basal lobe of the hammer is much shorter than the other lobe. The convoluted prostate branches to a short ejaculatory duct that is completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 15D). The large mucous gland bends at its free end. There is a single secondary bursa copulatrix.

Discussion: This record of *P. elegans* is the first since Bergh's original description (Bergh, 1905), which was based on one specimen. The type material seems to be lost: it is not present in the collections of the Zoologisk Museum, Copenhagen, where most of Bergh's remaining types are housed. Bergh described much of the anatomy of this species and illustrated the early whorls of the shell, the fringed gizzard plates, and a radular tooth. The species is autapomorphic for fringed gizzard plates, and is therefore easy to recognize. The large paired plates are most similar to those found in *P. angasi*, but the extensions are much larger, and the paired holes are close to each other. They are a modified version of the tricornered hat found in *P. aperta*, because the plates are slightly twisted along the

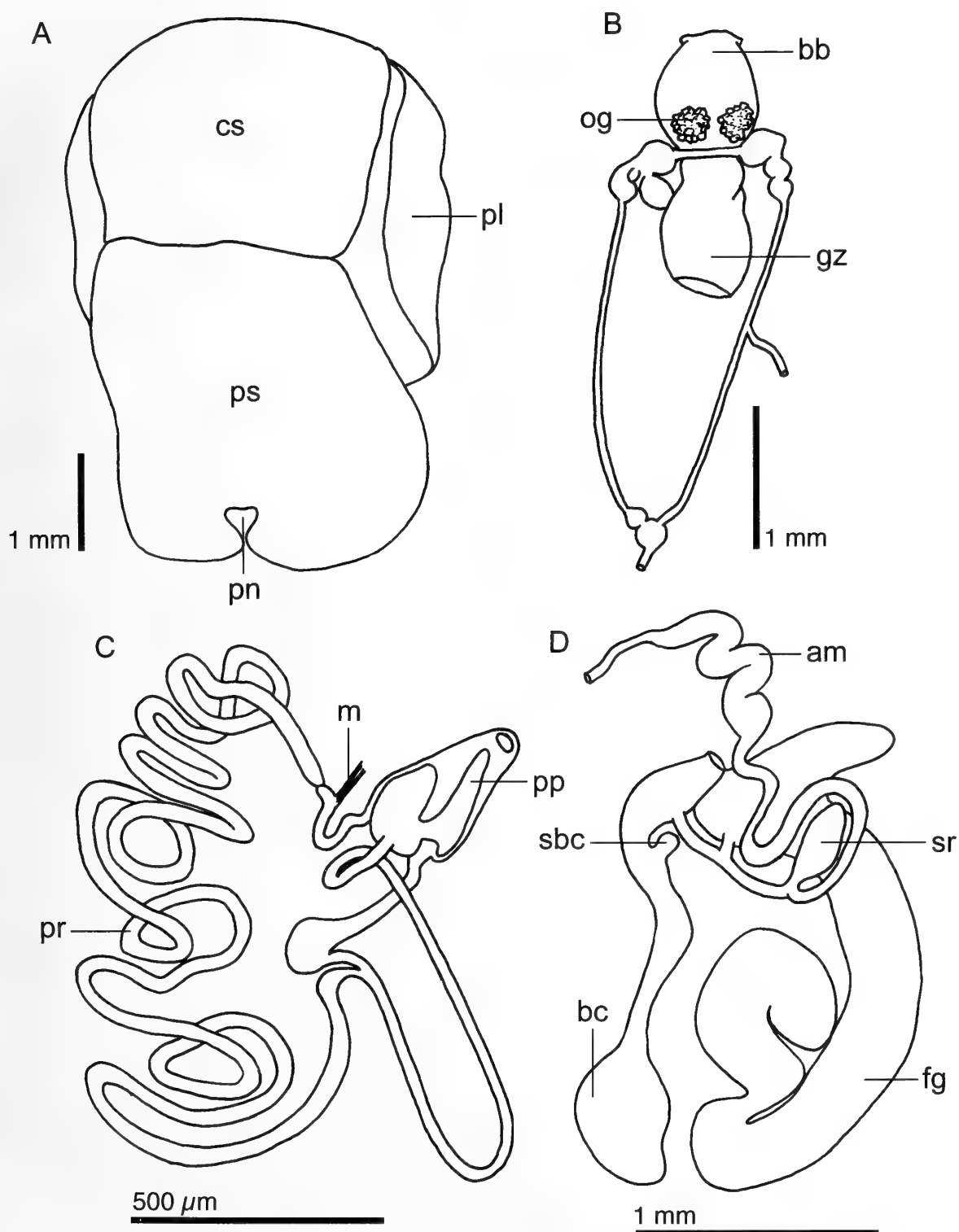


Figure 15. *Philine elegans* (CASIZ 083758). Anatomy. **A**, dorsal view of a living animal; **B**, anterior portion of the digestive system and nervous system; **C**, male reproductive system; **D**, female reproductive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cs**, cephalic shield; **fg**, female glands; **gz**, gizzard; **m**, muscle; **og**, oral gland; **pl**, parapodial lobe; **pn**, posterior notch; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

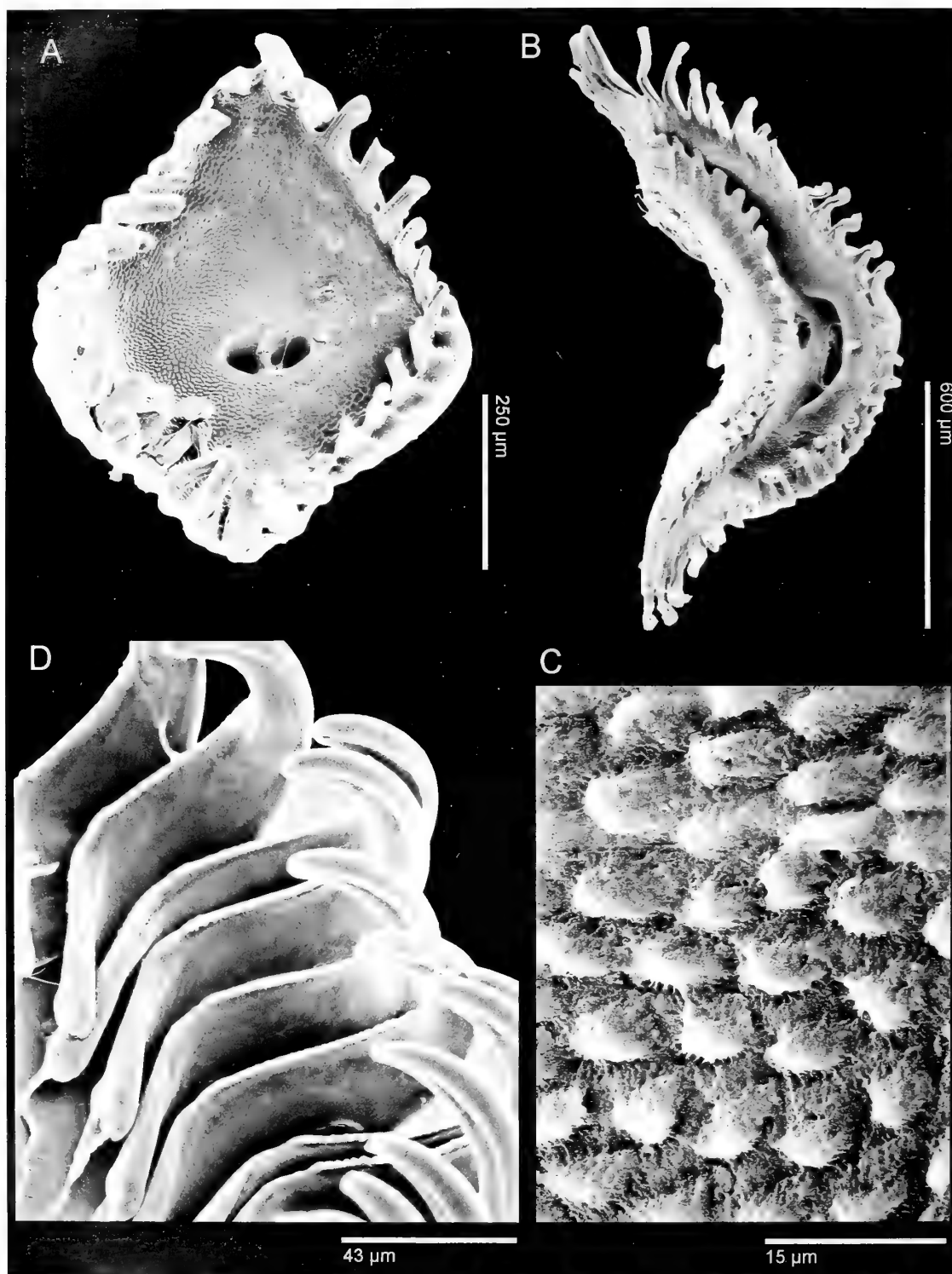


Figure 16. *Philine elegans* (CASIZ 083758), SEM photographs of internal hard structures: **A**, paired gizzard plate; **B**, unpaired gizzard plate; **C**, radular teeth; **D**, gizzard-plate microsculpture.

long axis. The smaller, unpaired plate is diamond-shaped, similar to that in *Philine habei* (Valdés, 2008), but with paired holes that are situated close to each other. The microsculpture of the plates is much smaller than in other species, although it is easier to see because of the deep, regular indentations.

The hammer head of the penial papilla has markedly unequal lobes, as in *P. puka*. The base of the papilla is round and lacks lobes.

The specimens were in Bouin's solution, which dissolved the shell. We based our assessment of the shell characters on Bergh's (1905) drawings.

Philine fenestra Price, Gosliner, and Valdés, sp. nov.

(Figures 17, 18)

Type material: Holotype: SAM, University of Cape Town Ecological Survey, Station SCD 129C, specimen 4–5 mm, coarse sand, 100 m depth, 34°48'S, 22°06'E, June 3, 1960. Paratypes: SAM, University of Cape Town Ecological Survey, Station FB 402A, False Bay, South Africa, three specimens, 4–6 mm, one dissected, fine sand, 31 m depth, 34°8.8'S, 18°33.5'E, May 16, 1961. University of Cape Town Ecological Survey, Station SCD 334 T-V, one specimen 3 mm, mud, 42 m depth, 34°02'S, 23°27'E, February 11, 1962. University of Cape Town Ecological Survey, Station SCD 129C, specimen 4–5 mm, coarse sand, 100 m depth, 34°48'S, 22°06'E, June 3, 1960. CASIZ 175004, one specimen, University of Cape Town Ecological Survey, Station SCD 186M, specimen 18 mm, mud, 97 m depth, 34°10'S, 23°32'E, November 30, 1960. CASIZ 175003, University of Cape Town Ecological Survey, Station NAD, two specimens 12–23 mm, one dissected, sand and mud, 175–200 m depth, 32°E, 29°37.5'S, 31°33'E, September 8, 1960.

Distribution: This species is known only from South Africa, where it has been found from False Bay to northern KwaZulu Natal.

Etymology: The name *fenestra*, a noun in apposition, is Latin for window and refers to the slits on the gizzard plates that are covered by a clear, hard (window-like) layer.

Type locality: False Bay, South Africa.

External morphology: The preserved animals are 3–12 mm in length. They are uniformly white with a long cephalic shield, and the posterior shield lacks a notch on its posterior end (Figure 17A). The parapodial lobes are narrow and not muscular.

Internal morphology: The whorls of the shell are tightly

coiled for this clade (Figure 18A). The shell surface is punctate throughout (Figure 18B).

There are two dorsal oral glands and one ventral oral gland. The radular formula is $18 \times 1.1.0.1.1$. The inner lateral teeth have a broad lateral ridge that is covered by 35–50 small denticles, and the outer lateral teeth are small, narrow, and elongate (Figure 18F). The gizzard is muscularized, but the three large plates are not covered with muscles. The equal-sized plates are roughly spindle-shaped with two long, lateral slits and smooth margins (Figure 18D, E). The slits are covered with a clear, hard layer that fractures easily when probed. The surface of the gizzard plates is textured with irregularly shaped polygons (Figure 18C). The esophagus does not expand into a crop posterior to the gizzard plates. The salivary glands are short.

The suprainestinal ganglion is located toward the anterior of the visceral loop, which is adjacent to, or adjoining, the fused pleural-parietal ganglion (Figure 17D).

The penial sac is barrel-shaped, and the tip of the papilla is hammer-shaped (Figure 17B). One lobe of the hammer is much shorter than the other lobe. The convoluted prostate branches to a short ejaculatory duct that is completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 17C). The large mucous gland has one lobe, and the free end bends. Two small and spherical secondary bursae branch off the primary, thin-walled bursa copulatrix. In addition, two adjoined semispherical bodies lie near the intersection of the bursa copulatrix and the female gland.

Discussion: The gizzard plates are by far the most easily recognized features of *P. fenestra*. They are equal in size and shape, with two long slits; one slit is on each edge of the concave surface. The only other species with similar slits is *P. auriformis*, but those slits are smaller and shallower. Furthermore, *P. auriformis* is larger and has a prominent notch in the center of the posterior end of the posterior shield. *Philine infundibulum* and *P. sarcophaga* also have slits of the gizzard plates, but they occur only on two of the three unequal plates.

Philine fenestra has two spherical and appressed bodies between the secondary bursae and the receptaculum seminis. The penial papilla is small and rests on top of two additional penial lobes, similar to those found in *P. sarcophaga* and *P. paucipapillata* (identified as *P. orientalis* by Morton & Chiu, 1990).

Philine finmarchica M. Sars, 1878

(Figures 19, 20)

Philine finmarchica Sars, 1878: 296, pl. 18, fig. 10a–d; pl. 12, fig. 1a, b. Marcus, 1974: 352, figs. 88–92.

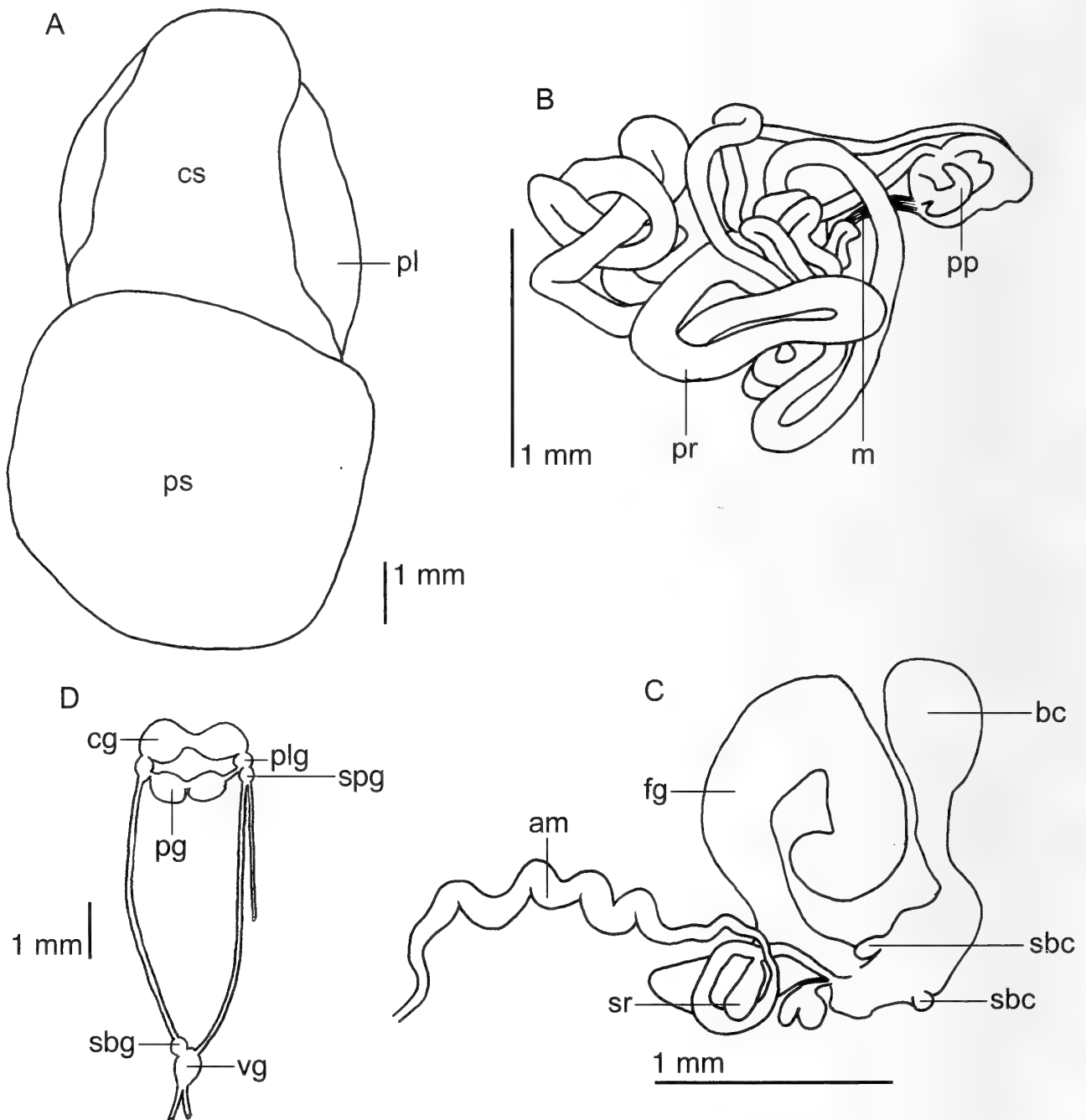


Figure 17. *Philine fenestra* (SAM FB 402A), anatomy: **A**, dorsal view of a preserved animal; **B**, male reproductive system; **C**, female reproductive system; **D**, nervous system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female gland; **m**, muscle; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sbg**, subintestinal ganglion; **spg**, suprainintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

Material: CASIZ 076660, one specimen, dissected, off Woods Hole, Massachusetts, 41°31'N, 70°40'W.

Distribution: This species is known from Cape Cod to

Greenland, the eastern Atlantic and Arctic Ocean (Marcus, 1974).

External morphology: The preserved animals are uniformly white and approximately 2 cm long. The

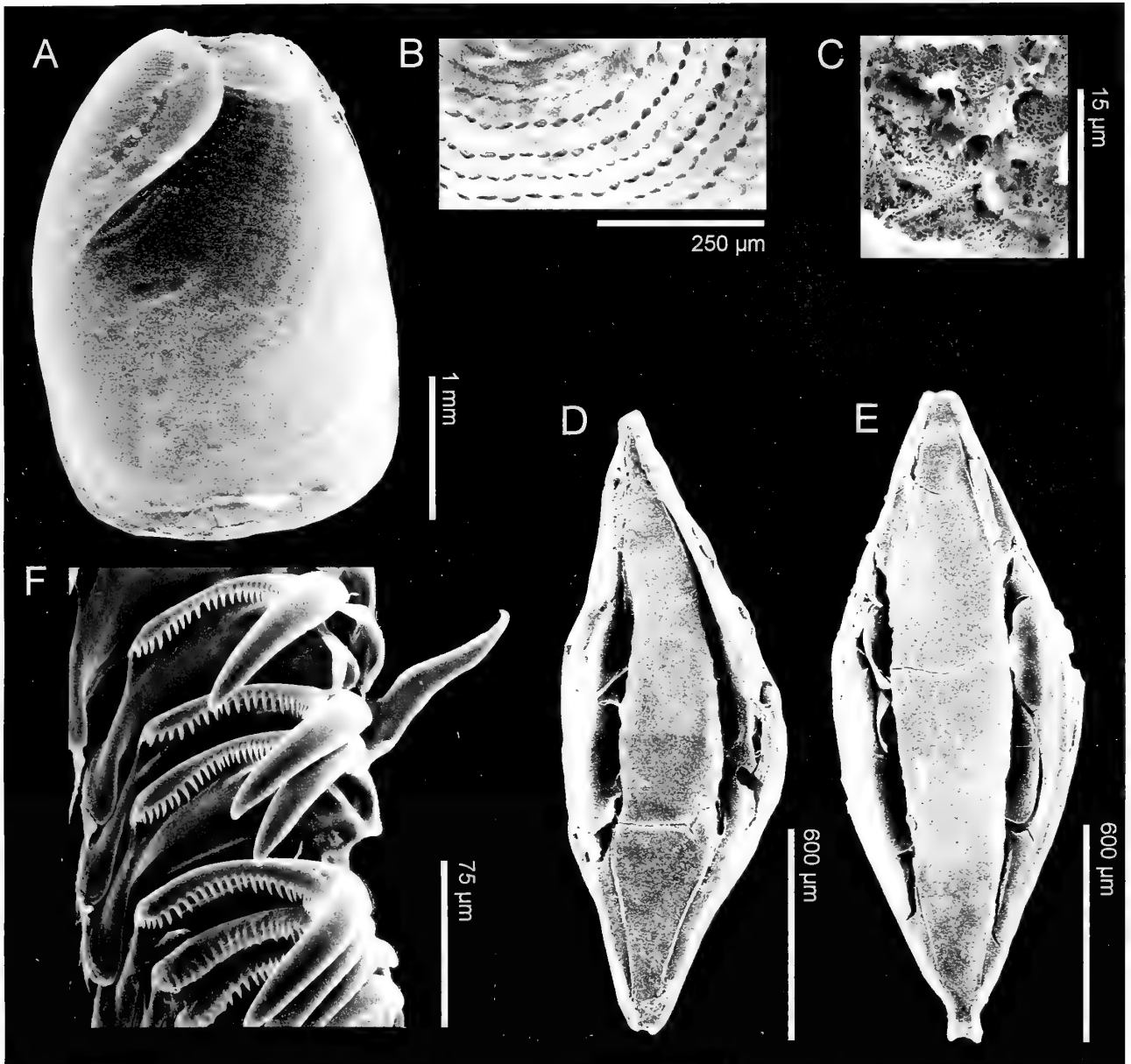


Figure 18. *Philine fenestra* (SAM FB 402A), SEM photographs of internal hard structures: **A**, ventral view of the shell; **B**, shell microsculpture; **C**, gizzard-plate microsculpture; **D**, **E**, gizzard plates; **F**, radular teeth.

cephalic and posterior shields are approximately the same size, and the parapodial lobes are narrow (Figure 19A). The posterior shield has a shallow notch.

Internal morphology: The shell is loosely coiled with a smooth surface.

There are two dorsal oral glands and one ventral oral gland. The radula has the formula of $15-16 \times 1.0.1$. The broad inner lateral teeth are covered with 72–80 elongate denticles. The esophagus does not expand into a crop posterior to the three, large, spindle-shaped and

equal-sized gizzard plates. The gizzard is muscularized (Figure 19E), but the three large, equal-sized plates are not covered with muscles. The gizzard plates (Figure 20) lack pores and slits. The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior suprainestinal ganglion (Figure 19C). The genital ganglion is fused to the visceral ganglion and adjacent to the subintestinal ganglion.

The penial papilla is hammer-shaped with lobes that are almost equal in size (Figure 19B). The ejaculatory

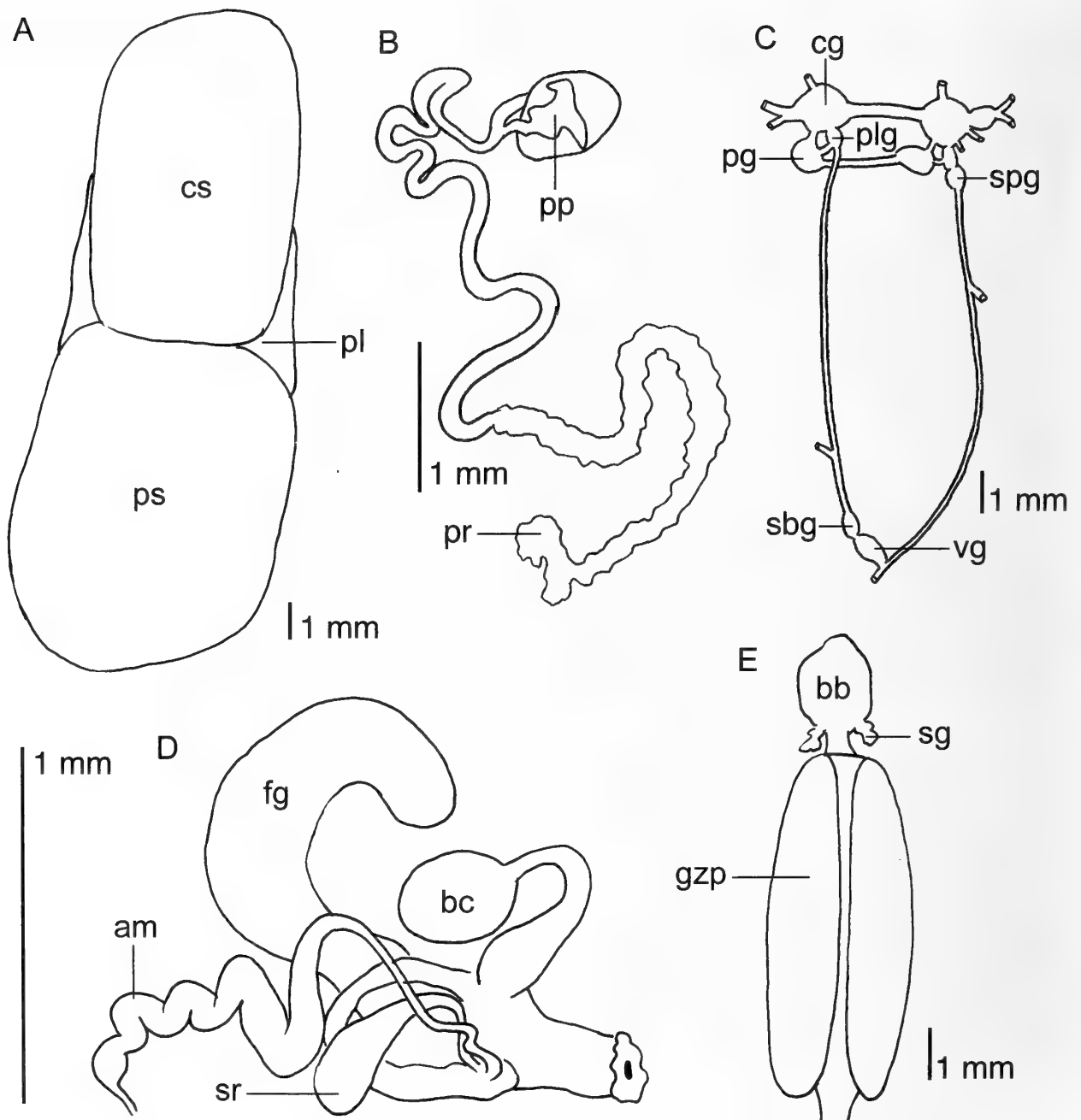


Figure 19. *Philine finmarchica* (CASIZ 076660) anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, nervous system; **D**, female reproductive system; **E**, anterior portion of the digestive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **gz**, gizzard plate; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **sg**, salivary gland; **spg**, suprainintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

duct has a very short branch that connects to the base of the penial papilla. The distal portion of the prostate is nodular, elongate, and simple. The convoluted ampulla (Figure 19D) narrows into the hermaphroditic

duct, at the side of which branches the single receptaculum seminis. The bursa copulatrix is large with a wide duct that joins the genital atrium. There is no secondary bursa copulatrix.



Figure 20. *Philine finmarchica* (CASIZ 076660). SEM photograph of a gizzard plate.

Discussion: *Philine finmarchica* lacks many of the characters shared by the other species within the *P. aperta* clade. The prostate, for example, is simple and nodular instead of convoluted and smooth, the gizzard plates are lenticular instead of spindle-shaped, and the gizzard plates lack slits or pores. However, the penial papilla illustrated here and by Marcus (1974:fig. 92) is clearly hammer-shaped with more or less equal lobes, similar in morphology to that of *P. aperta*. A very short ejaculatory duct is present, but it is much less developed than in any other member of the *P. aperta* clade.

Philine habei Valdés, 2008

(Figures 21, 22)

Philine habei Valdés, 2008:717–720, fig. 64A, 65B.

Material: MNHN (no specimen number), Station CP 15588, specimens (one dissected), 580–593 m, Tonga: Cheal nord Nomuka 20°10'S, 174°43'W.

Distribution: *Philine habei* is known from New Cale-

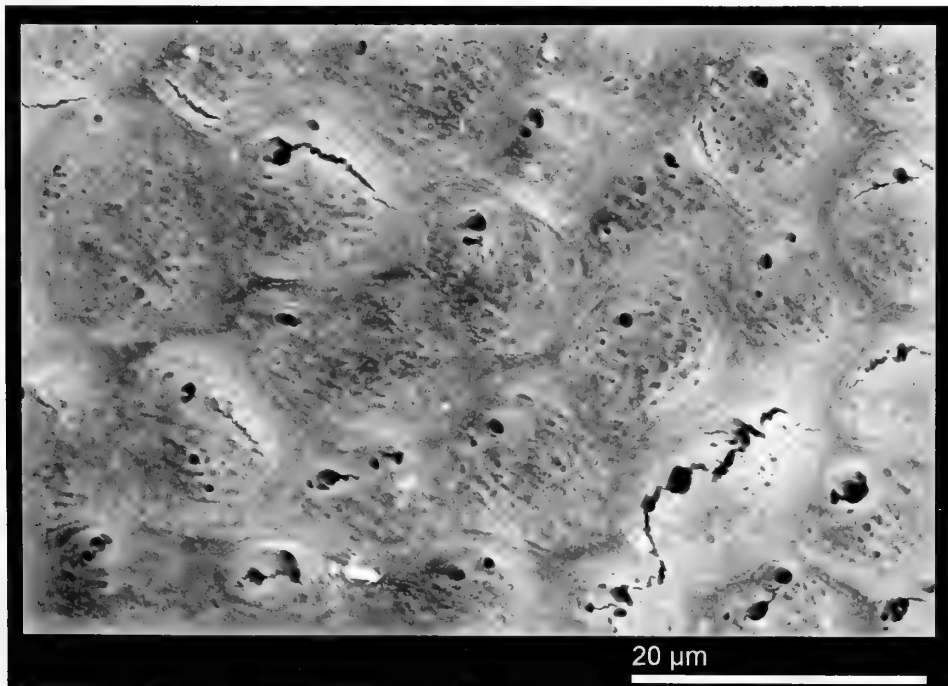


Figure 21. SEM photograph of the gizzard-plate microsculpture of *P. habei* (MNHN no specimen number).

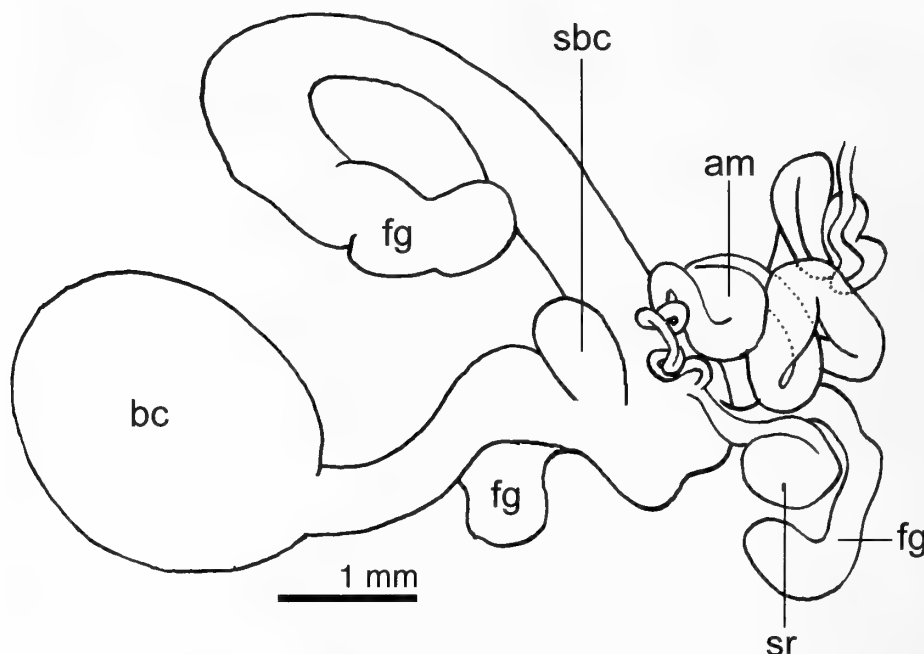


Figure 22. Female reproductive organs of *P. habei* (MNHN no specimen number). Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **fg**, female glands; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

donia, Fiji, Tonga, Vanuatu, and Wallis and Futuna Islands from 250–688 m. The type locality is in Fiji.

External morphology: The living animal is uniformly white and approximately 3 cm long. The cephalic shield is slightly longer than the posterior shield. The posterior shield lacks a posterior notch. The parapodial lobes are narrow.

Internal morphology: The shell is particularly fragile and lacks punctuation. It has a high rate of expansion.

There are no dorsal or ventral oral glands. The buccal bulb is small. The radular formula is $16 \times 1.0.1$. The lateral teeth have a broad base that lacks denticles. The crop is indistinct. The gizzard is muscularized, but the plates are not covered with muscles. The spindle-shaped gizzard plates all have two large pores; their margins are smooth. The unpaired plate is smaller than the paired plates. The plate microsculpture consists of a meshwork of irregularly shaped polygons (Figure 21). The salivary glands are small.

The fused pleural-parietal ganglion is adjacent to the anterior suprainestinal ganglion. The genital ganglion remains distinct from the visceral ganglion, but the visceral ganglion is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has markedly unequal lobes, is supported by a stout stalk, and distends the base of the pyriform penial sac over the convoluted prostate. The convoluted prostate branches to the ejaculatory duct, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is

short, but it is not surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 22), at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes. There is one secondary bursa copulatrix.

Discussion: *Philine habei* (Valdés, 2008), along with *P. puka*, has large, elongate pores on the gizzard plates. The plate microstructure in *P. habei* however lacks the many indentations present in *P. puka*. *Philine habei* differs from *P. puka* in that it lacks denticles on the inner lateral teeth.

The penial papilla is similar to that found in *P. argentata* and *P. quadripartita* because of the unequal lobes on the large hammer head and an additional lobe branching from the base of the stalk.

Philine infundibulum Dall, 1889

(Figures 23, 24)

Philine infundibulum Dall, 1889:57. Marcus, 1974:355, figs. 93–97.

Material: CASIZ 079484, one specimen, dissected, off Woods Hole, Massachusetts. CASIZ 076159, one specimen, dissected, off Woods Hole.

Distribution: Known from the western Atlantic from

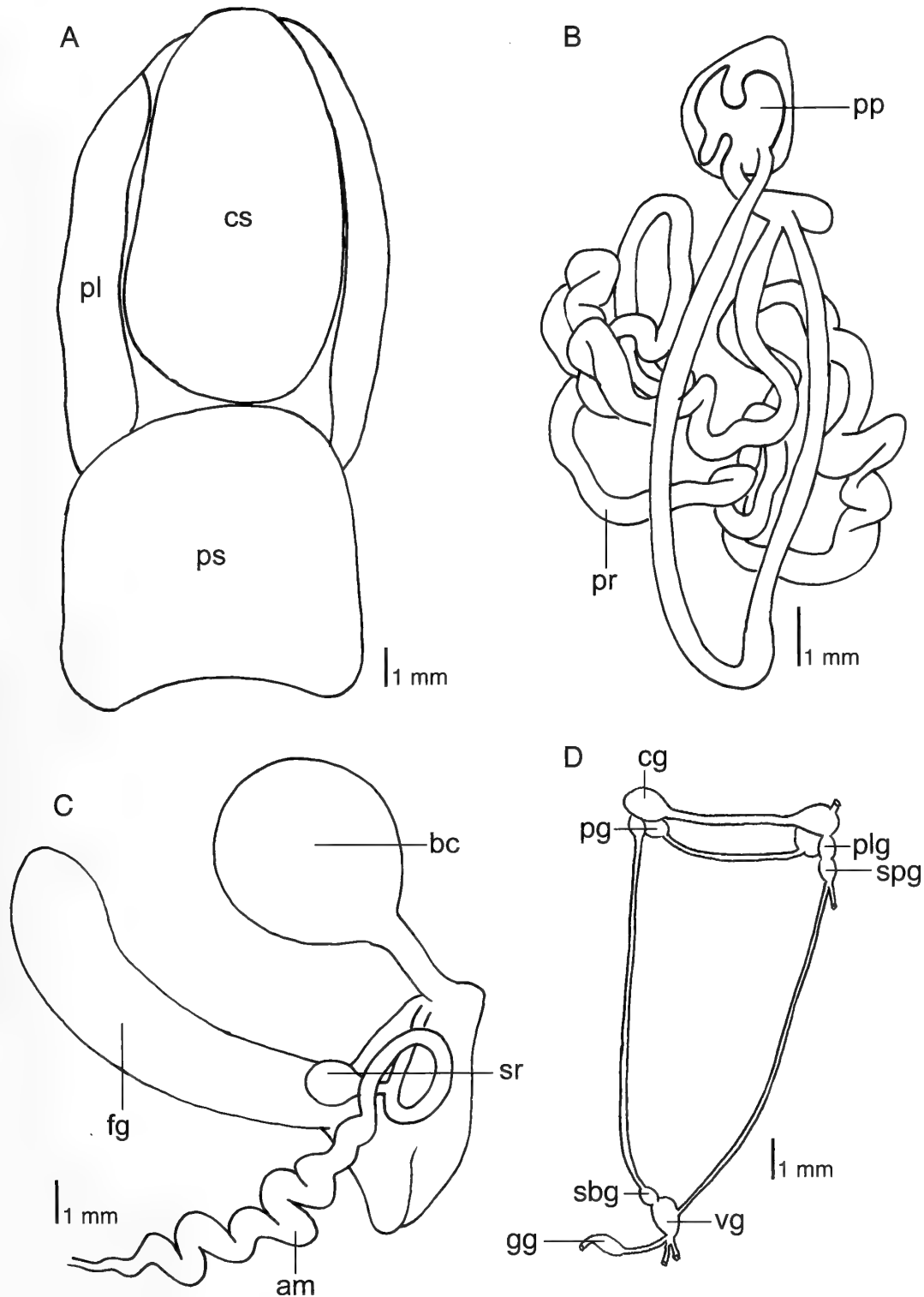


Figure 23. *Philine infundibulum* (CASIZ 076159), anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, female reproductive system; **D**, nervous system; **E**, anterior portion of the digestive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **gz**, gizzard; **m**, muscle; **og**, oral gland; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **sg**, salivary gland; **spg**, suprainintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

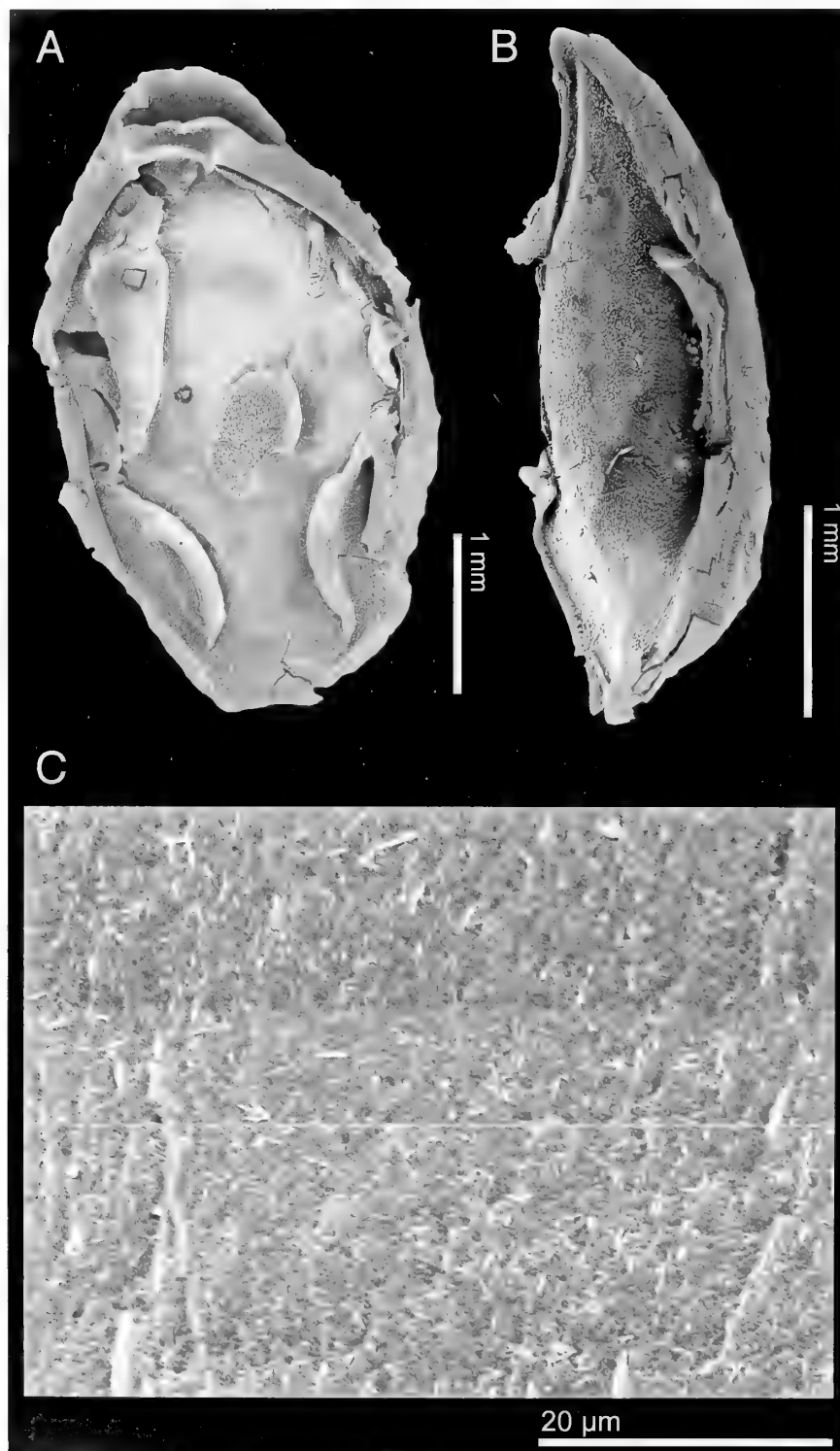


Figure 24. *Philine infundibulum* (CASIZ 076159), SEM photographs of internal hard structures: **A**, paired gizzard plate; **B**, unpaired gizzard plate; **C**, gizzard-plate microsculpture.

northern Brazil to Cape Cod, Massachusetts (Marcus, 1974; present study).

External morphology: The preserved animals are uniformly white and approximately 3 cm long (Marcus & Marcus, 1967). The cephalic shield is longer than the posterior shield (Figure 23A). The parapodial lobes are thin and flimsy. It is uncertain whether the posterior shield is notched or unnotched in the two dissected specimens.

Internal morphology: The smooth shell is relatively tightly coiled for a *Philine*.

There are two dorsal oral glands and one ventral oral gland. The buccal bulb and radula are reduced, and the radular formula is $20-24 \times 1.1.0.1.1$, with 28–37 denticles on the inner side of the broad tooth. The radula of the present specimen was not examined by SEM because it was already mounted on a microscope slide. The crop is indistinct. The gizzard is muscularized, but the three large plates are not covered with muscles. The paired plates (Figure 24B) are spindle-shaped with a single large slit on the concave edge. The unpaired plate (Figure 24A) is slightly smaller than the other two; it is rhomboidal and lacks slits. The high magnification of the gizzard plates reveals that they lack any obvious microstructure (Figure 24C). The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior suprainestinal ganglion (Figure 23D). The genital ganglion remains distinct from the visceral ganglion, but the visceral ganglion is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has subequal lobes and rests within the penial sac (Figure 23B). The ejaculatory duct branches from the convoluted prostate branches, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is long, but it is not surrounded by the convoluted prostate. The prostate is smooth.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 23C), at the side of which branches a single, long and narrow receptaculum seminis. The female gland is relatively small for this clade. The bursa copulatrix is large, and there is a single secondary bursa copulatrix.

Discussion: The simple, hammer-shaped penial papilla is most similar to that of *P. auriformis* because the lobes are subequal and small, resting on a short stalk. The plates are all spindle-shaped and lack pores. The paired plates are more tapered than the unpaired, and as in *P. sarcophaga*, one edge is much flatter than the other edge. They also have a single large slit on the edge of the rounded side. *Philine sarcophaga* and *P. fenestra* also have slits, but the slits in *P. fenestra* are all of the same size, and they line the edges of all three equally

sized plates. *Philine infundibulum* is more similar to *P. sarcophaga*, which also has two paired plates. The unpaired plate in both of these species is rhomboidal, but the plate in *P. infundibulum* lacks the rounded anterior knob present in *P. sarcophaga*.

The gizzard-plate microstructure in *P. infundibulum* is difficult to interpret because our specimen is poorly preserved.

Philine orientalis A. Adams, 1854

(Figures 2E, 25–29)

Philine orientalis A. Adams in Adams and Adams, 1854–1858:94.

Philine argentata Gould, 1859: 139 syn. nov.

Philine japonica Lischke, 1872: 105, syn. nov.

Philine striatella Tapparone-Canefri, 1874:109, syn. nov.

Material: Types of *P. orientalis*, BMNH, H. Cuming collection, accession 1829, shell and gizzard plates, “eastern seas.” CASIZ 078442, nine specimens, two dissected, 1 m depth on sand bar at night, 100 m E of Matiara Hotel, Langkawi Island, Strait of Malacca, Malay Peninsula, Malaysia, 6°26'N, 99°48'E, collected by T. M. Gosliner. BMNH 1996409, three specimens (all dissected), Nagasaki, Japan. CASIZ 082054, 20 specimens, one dissected, 80–100 fathoms, southwest of Kao-Hsiung into South China Sea, Taiwan, October 12, 1972, collected by F. B. Steiner. CASIZ 174126, four specimens, two dissected, Bodga Harbor, California, July 1998, Michelle Chow.

Distribution: *Philine orientalis* was originally described from “eastern seas,” whereas *P. argentata* was described from Hakodate Bay, Japan, 2–6 fathoms. It is also known from Malaysia, Japan, and Taiwan, and it has been introduced in central California (present study).

External morphology: The living animal is uniformly white (Figure 2E) and approximately 2.5–4 cm in length. The cephalic shield is longer than the posterior shield, and the parapodial lobes are thick and muscular (Figures 25A, 26A). A notch may be present or absent on the posterior shield but seems to be absent in poorly preserved specimens.

Internal morphology: The shell is loosely to tightly coiled and is either smooth or punctate with an ovate perimeter (Figures 27A, B; 28A, B; 29A).

There are two appressed ventral oral glands, and two dorsal oral glands. The buccal mass is small, and the radula has the formula $17-22 \times 1.0.1$, with 35–42 small denticles on the broad inner lateral tooth (Figures 28E, 29E). There is no crop. The gizzard is muscularized, although the plates are not covered with muscles

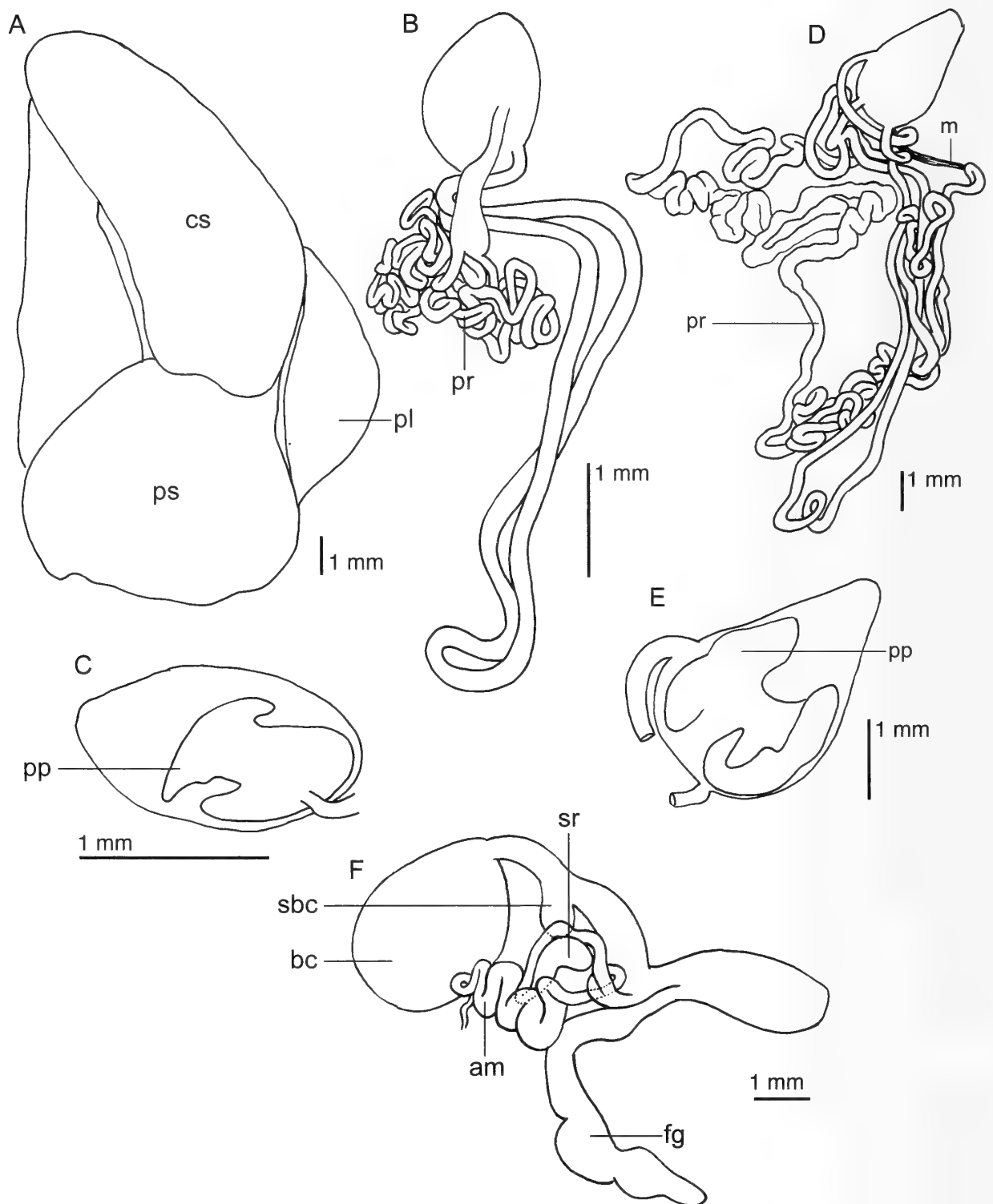


Figure 25. *Philine orientalis* anatomy, specimens from Nagasaki, Japan (BMNH 1996409 [A–C, F]) and Tomales Bay, California (CASIZ 082054 [D, E]). A, dorsal view of a living animal; B, male reproductive system; C, penis; D, male reproductive system; E, penis; F, female reproductive organ. Abbreviations: am, ampulla; bc, bursa copulatrix; cs, cephalic shield; fg, female glands; m, muscle; pl, parapodial lobe; pp, penial papilla; pr, prostate; ps, posterior shield; sbc, secondary bursa copulatrix; sr, receptaculum seminis.

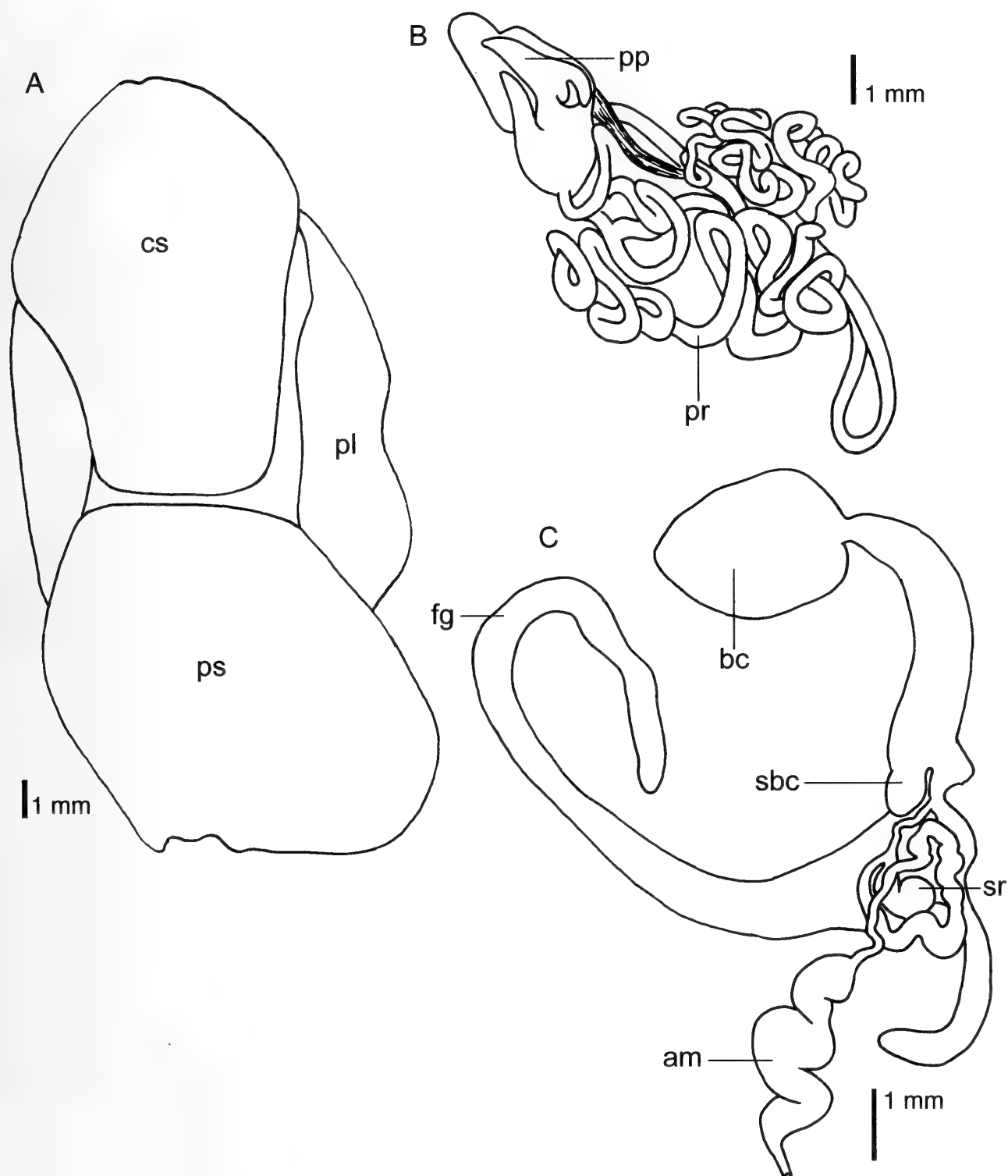


Figure 26. *Philine orientalis* anatomy, specimen from Malaysia, CASIZ 078442: **A**, preserved animal; **B**, penis; **C**, female reproductive system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **fg**, female glands; **pl**, parapodial lobe; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

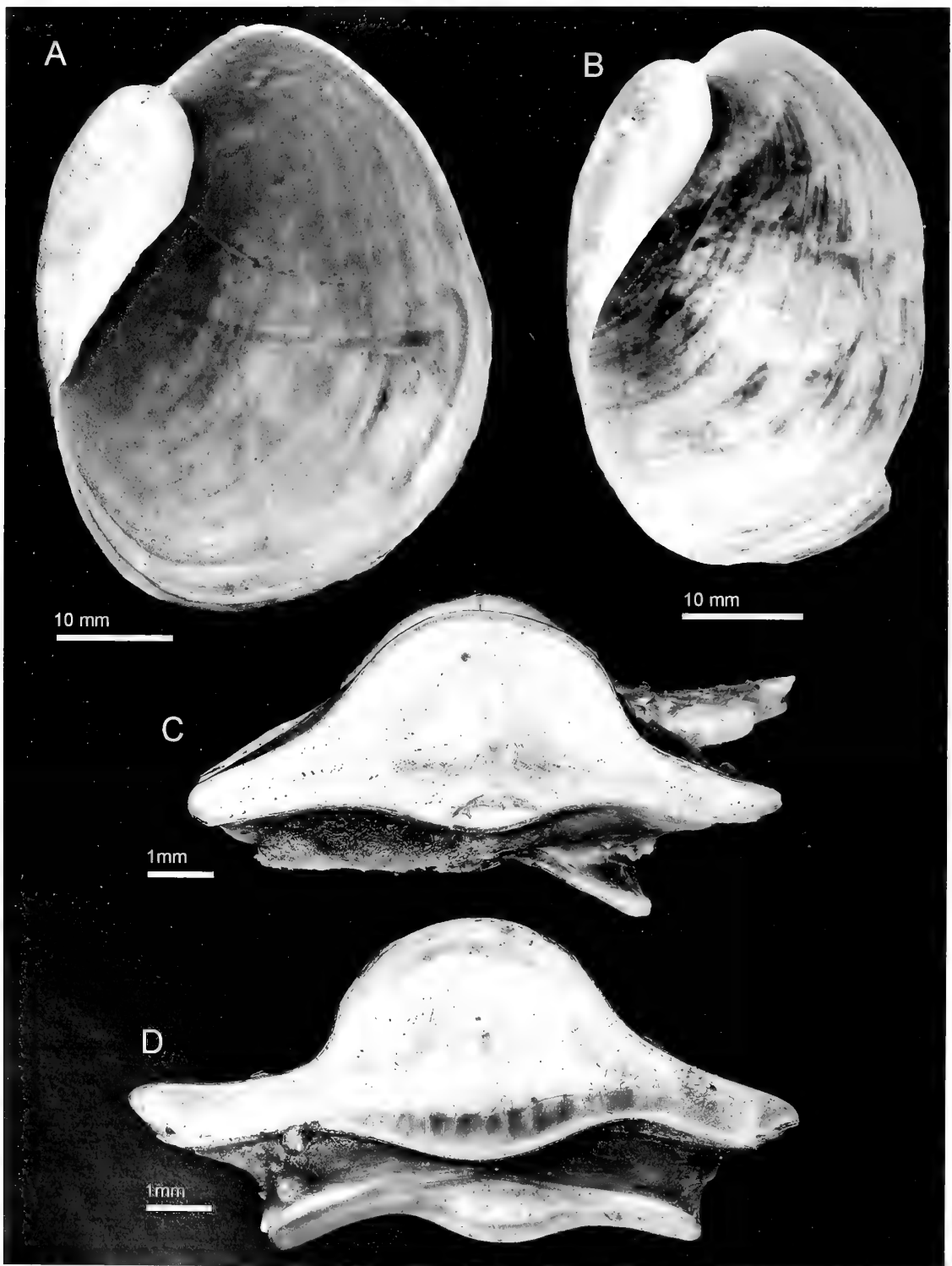


Figure 27. *Philine orientalis*, light photographs of the type specimens, BMNH, H. Cuming collection, accession number 1829. A, B, ventral view of the shells; C, D, gizzard plates.

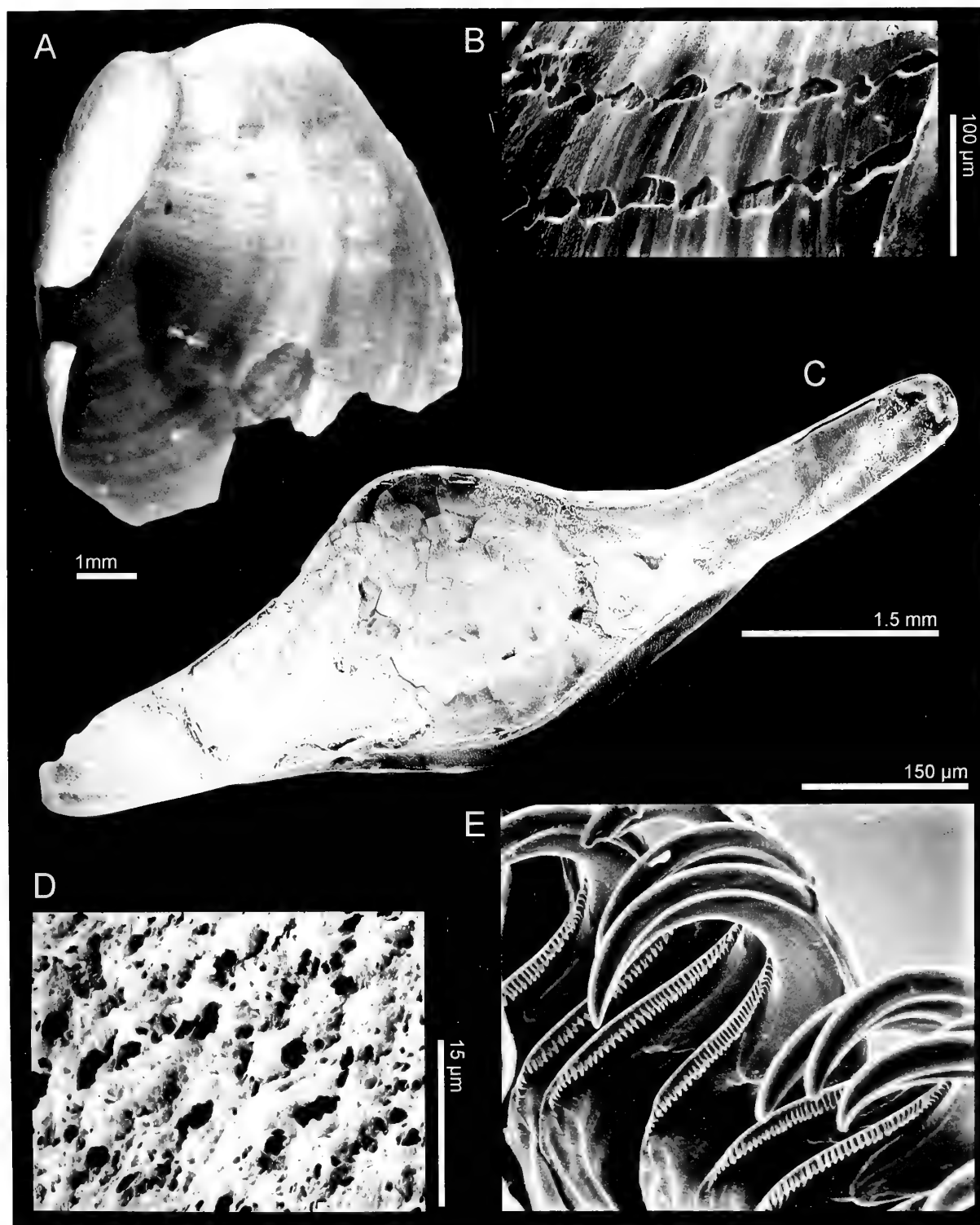


Figure 28. *Philine orientalis* (BMNH 199609), specimen from Nagasaki, Japan, photographs of internal hard structures. **A**, light photograph of a ventral view of the shell; **B**, SEM photograph of the shell microsculpture; **C**, SEM photograph of a gizzard plate; **D**, SEM photograph of the gizzard-plate microsculpture; **E**, SEM photograph of the radular teeth.

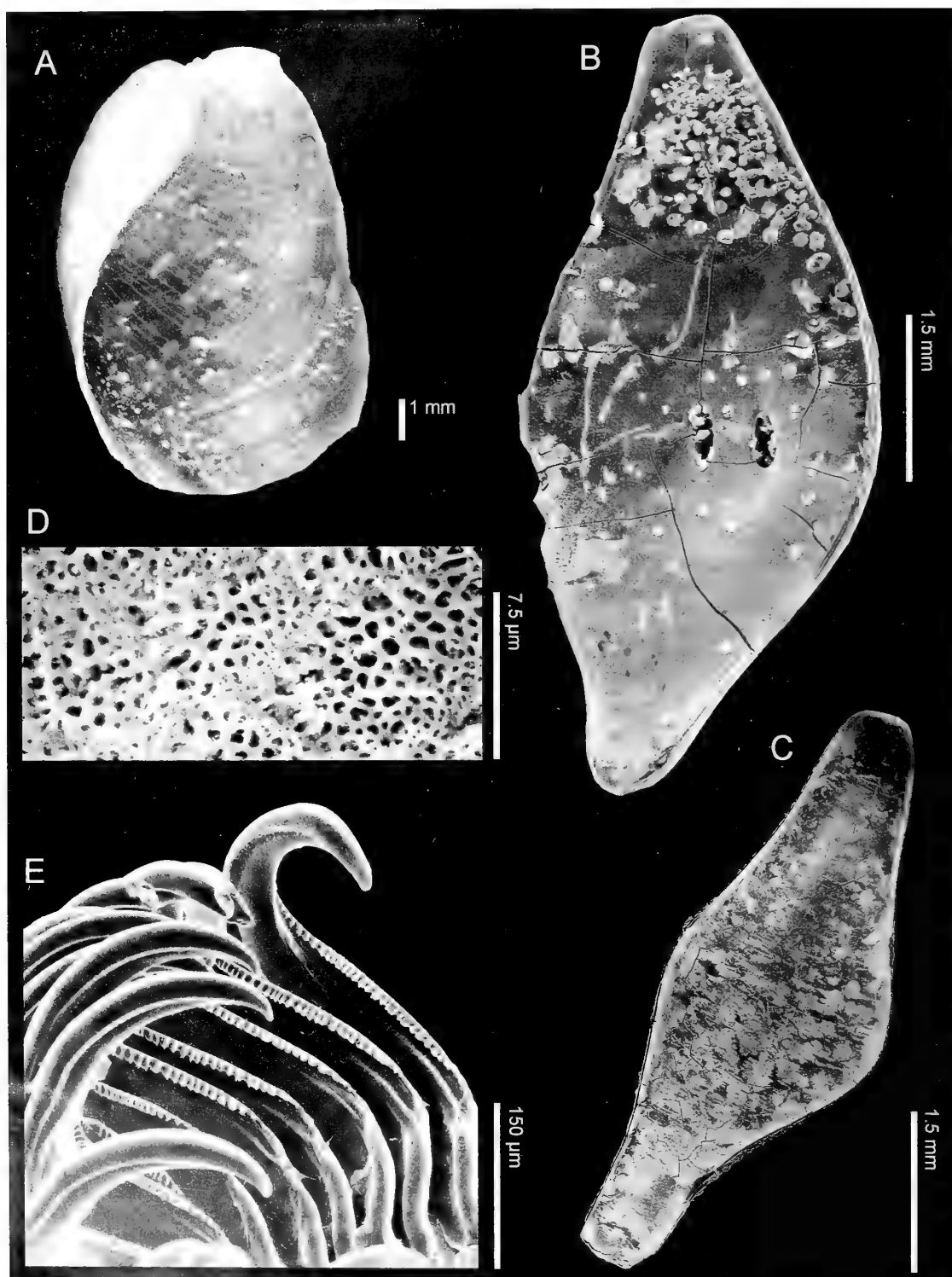


Figure 29. *Philine orientalis* (CASIZ 174126), specimen from Bodega Harbor, California, photographs of internal hard structures: A, light photograph of a ventral view of the shell; B, SEM photograph of a paired gizzard plate; C, SEM photograph of the unpaired gizzard plate; D, SEM photograph of the gizzard-plate microstructure; E, SEM photograph of the radular teeth.

(Figure 27C, D). The three spindle-shaped plates have small-to-medium, shallow pores (Figures 27C, D; 28C; 29B, C). The two paired plates are broad and fill the entire anterior portion of the body. The unpaired plate is much shorter and narrower. The microsculpture consists of regularly arranged polygons (Figures 28D, 29D). The salivary glands are short.

The suprainestinal ganglion is located toward the anterior of the visceral loop and is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off halfway between the suprainestinal ganglion and the visceral ganglion. The subintestinal ganglion is fused to the visceral ganglion, but the genital ganglion remains distinct.

The penial sac is ovoid, and the penial papilla is hammer-shaped with subequal lobes and is supported above the cushion-shaped base by a stalk (Figures 25C, E; 26B). The base of the penial papilla does not distend the wide penial sac. The convoluted prostate branches into a long ejaculatory duct that extends to, or far beyond, the buccal mass to the gizzard, but it is completely uncovered by the prostate (Figures 25B, D; 26B). The prostate seems especially granular.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figures 25F, 26C). The large mucous gland has one lobe above the albumen gland, and the free end bends. There is a single secondary bursa copulatrix.

Discussion: There has been much confusion surrounding the identification of *P. orientalis*, based largely on the facts that the type material was described only as collected from the vague locality “eastern seas” and that no complete description of the anatomy had been published. The type material in the BMNH consists of a shell and three gizzard plates. The material agrees with specimens we have studied here from Japan, Malaysia, Taiwan, and California. All of these specimens have two large paired gizzard plates and a narrow, shorter unpaired plate.

The pore size on the gizzard plates of this species are more variable than those of any of the other species we have described. The type specimens (Figure 27C, D), the Malaysian specimens that we have studied, and the Japanese specimens that we have studied (e.g., Figure 28C) have small pores. However, the specimen from Bodega Harbor, California, that we depict in Figure 29B has slightly larger pores on the paired plates.

Philine orientalis is the oldest available name for these taxa, and *P. argentata* and its synonyms should be regarded as junior synonyms of *P. orientalis*. We agree with other authors who have synonymized *P. argentata*, *P. japonica*, and *P. striatella* (e.g., Kuroda et al., 1971). Although the descriptions of these taxa are

largely incomplete, there seems to be a single large, shallow-water species in Japanese waters, the type locality of all three species. It seems that *P. orientalis* has been introduced into San Francisco Bay and the nearby estuaries of Tomales Bay and Bodega Bay, and it was first recorded by Gosliner & Williams (2007) as *P. sp.* As with *P. auriformis*, this species was probably introduced by discharge of ballast water.

Specimens identified as *P. orientalis* from Hong Kong (Morton & Chiu, 1990) and Cambodia (present study) are morphologically distinct from those found in Malaysia, Japan, and Taiwan (present study) and represent a distinct species described here as *P. paucipapillata*. Throughout the Pacific waters of Southeast Asia, there seem to be two distinct members of the *Philine aperta* clade: *P. orientalis* and *P. paucipapillata*. The gizzard plates of *P. orientalis* have two smaller pores, similar to those in *P. paucipapillata* from Hong Kong and Cambodia, but the ends of the spindle are proportionately much longer in *P. orientalis*. Both have the regular polygon microstructure of the gizzard plates. The penial papilla of *P. orientalis* has two hammer-shaped subequal lobes similar to that of *P. habei* (Valdés, 2008) and *P. quadripartita*, but it differs markedly from that of *P. paucipapillata*. In that species, the penial papilla is rounded without the two elaborate hammer-shaped arms found in *P. orientalis*.

The specimen of *P. argentata* described in Habe (1950) as *Yokoyamaia argentata*, has a “hint of spines that are extensions of shell ribs” (Gosliner, 1988). Habe’s material is most likely a different species.

Philine paucipapillata Price, Gosliner, and Valdés,
sp. nov.

(Figures 30, 31)

Philine orientalis Adams and Adams, 1854–1858: 39,
Morton and Chiu, 1990:289, figs. 3, 4, misidentification.

Type material: Holotype, CASIZ 174143, Kampote and Prek Romeas, Cambodia, fish landings, March 29 and April 6, 2006, Tyson Roberts. Paratypes, CASIZ 174144, three specimens, one dissected, Kampote and Prek Romeas, Cambodia, fish landings, March 29 and April 6, 2006, Tyson Roberts.

Additional material: BMNH 1996410, more than 10 specimens, dissected, Tolo Channel, Hong Kong, collected by J. D. Taylor.

Distribution: Known from Tolo Channel, Hong Kong (Morton & Chiu, 1990) and Cambodia (present study).

Etymology: The name *paucipapillata* refers to the fact that this species has a penial papilla that is much smaller than that of other members of this clade.

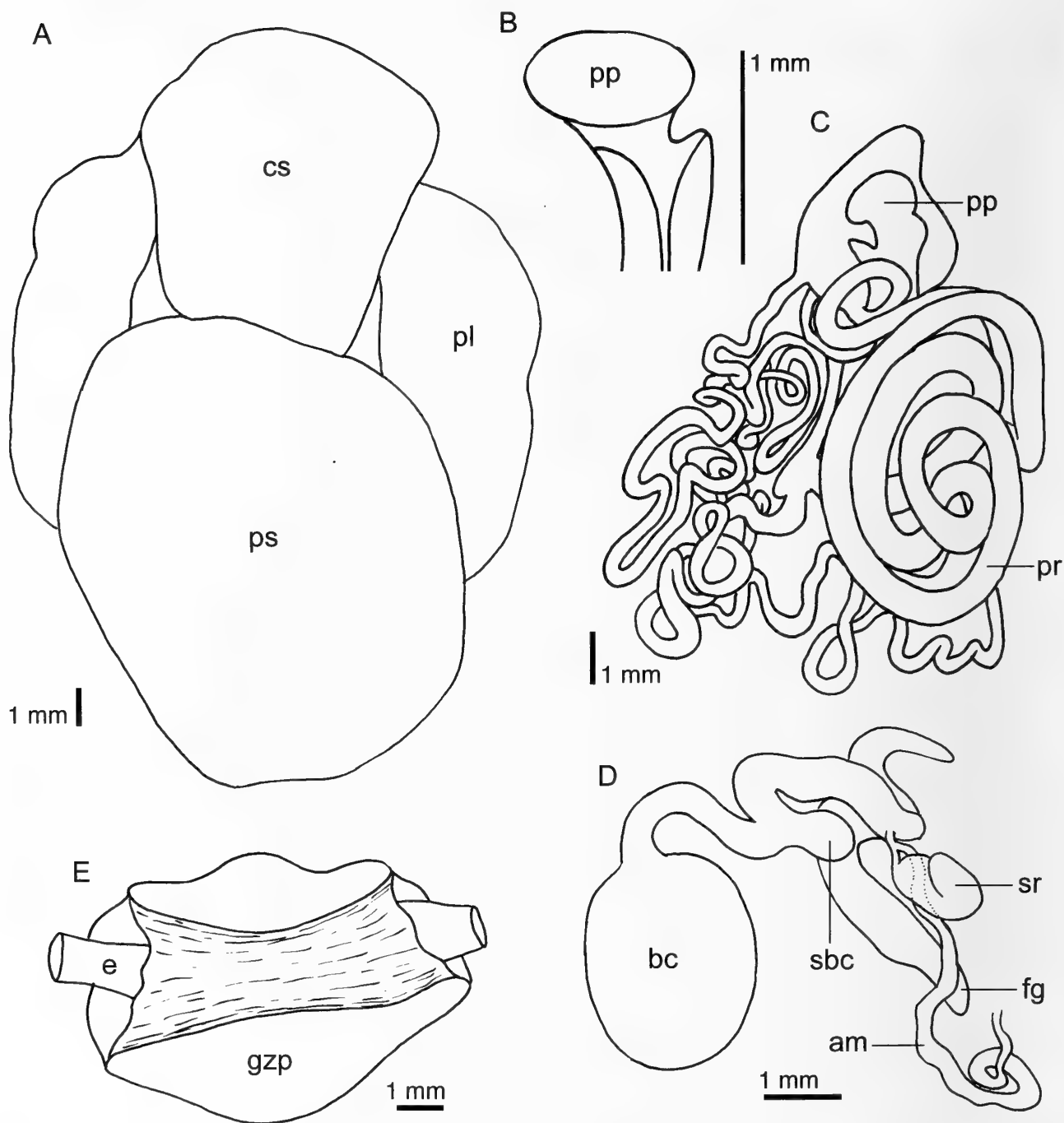


Figure 30. *Philine paucipapillata* (BMNH 1996410), anatomy: **A**, dorsal view of a preserved animal; **B**, penis; **C**, male reproductive system; **D**, female reproductive system; **E**, gizzard. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **e**, esophagus; **fg**, female glands; **gzp**, gizzard plate; **pl**, parapodial lobe; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

Type locality: Kampote and Prek Romeas, Cambodia.

External morphology: The living animal is uniformly white and about 4–5 cm in length. The cephalic shield is

longer than the posterior one (Figure 30A). The parapodial lobes are thick and muscular, and the posterior notch is very shallow to absent.

Internal morphology: The shell (Figure 31A) is tightly

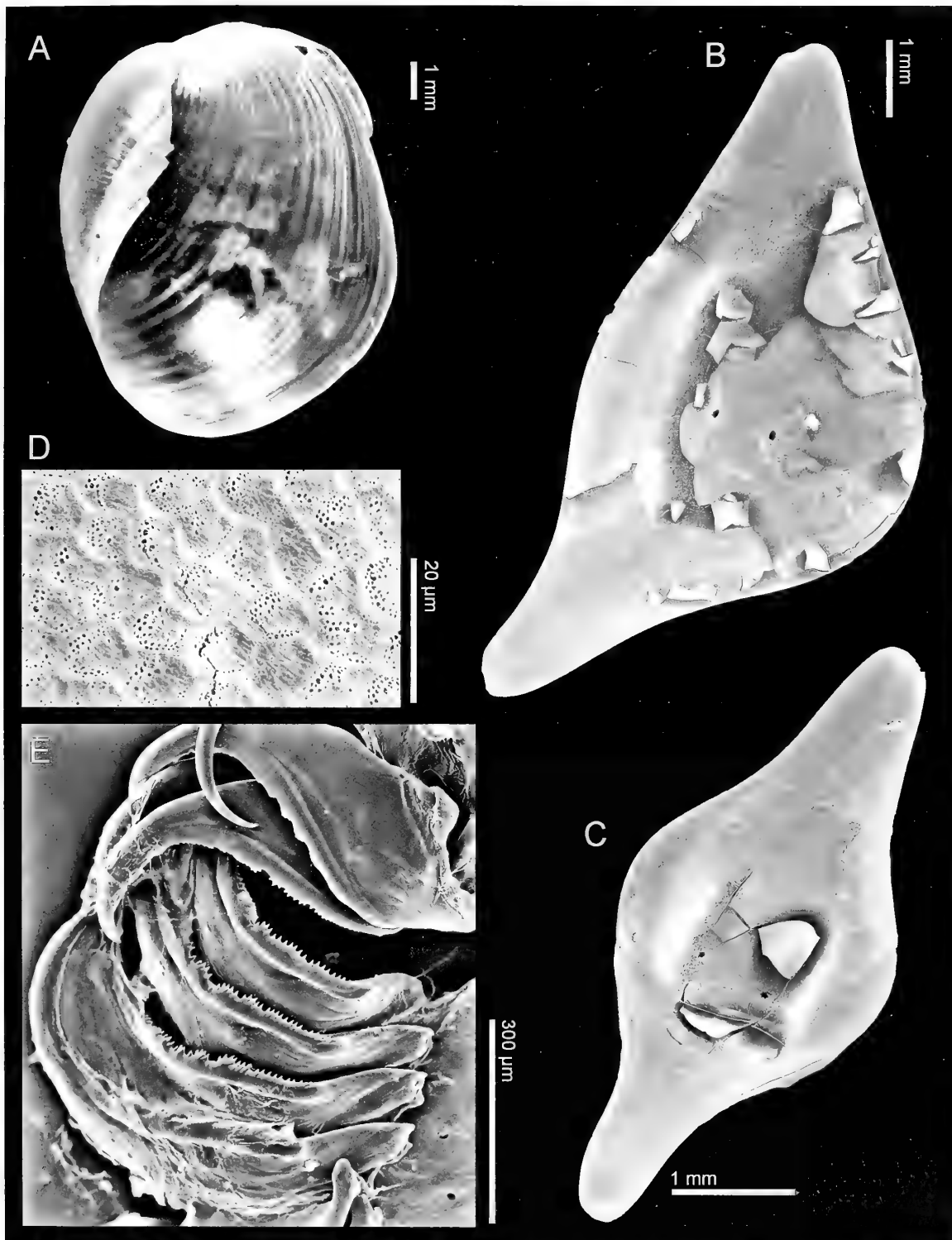


Figure 31. *Philine paucipapillata* (BMNH 1996410), photographs of internal hard structures: **A**, light photograph of a ventral view of the shell; **B**, SEM photograph of a paired gizzard plate; **C**, SEM photograph of the unpaired gizzard plate; **D**, SEM photograph of the gizzard-plate microsculpture; **E**, SEM photograph of the radular teeth.

coiled for a *Philine* and has an ovate perimeter. The surface of the shell is smooth.

There are two, appressed ventral oral glands and two dorsal oral glands. The buccal mass is small, and the radula has the formula $18-22 \times 1.0.1$. The broad inner lateral tooth (Figure 31E) has 38–40 denticles that are arranged in an irregular manner, with an uneven edge that undulates along the masticatory margin. There is no crop. The gizzard (Figure 30E) is muscularized, although the plates are not covered with muscles. The three spindle-shaped plates have minute, shallow pores (Figure 31B, C). The two paired plates (e.g., Figure 31B) are broad and fill the entire anterior portion of the body. The unpaired plate (Figure 31C) is much narrower. The plate microsculpture (Figure 31D) consists of irregularly shaped polygons. The salivary glands are short.

The suprainestinal ganglion is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off from halfway between the suprainestinal ganglion and the visceral ganglion. The genital ganglion is distinct. The subintestinal ganglion is fused to the visceral ganglion.

The penial sac is ovoid, and the penial papilla is hammer-shaped but with short rounded lobes giving the entire papilla a club-shaped appearance (Figure 30B, C). The base of the papilla rests on two lobes that form the base of the penis. The tightly coiled prostate branches to the ejaculatory duct. The ejaculatory duct is highly convoluted. Its posterior end is connected to the penial sac by a short muscle. The prostate is smooth rather than granular.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 30D), at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes above the albumen gland, and the free ends bend. There is single secondary bursa copulatrix.

Discussion: This new species has been previously considered as *P. orientalis* (Morton & Chiu, 1990), but the distinctions in the bulbous penial papilla and the undulating denticular margin on the masticatory border of the inner lateral teeth clearly indicate that it is a distinct species. These important characters distinguish this species from all other described *Philine*.

Philine puka Price, Gosliner, and Valdés, sp. nov.

(Figures 32, 33)

Type material: Type material: Holotype: CASIZ 175005, one specimen, 200 m depth, Ewa, off the coast of Barbers Point, Oa'hu, Hawai'i, collected April 27, 1973 by D. Bonar. Paratypes: CASIZ 082128, three specimens, two dissected, 200 m depth, Ewa, off the coast of Barbers Point, Oa'hu, Hawai'i, collected April 27, 1973 by D. Bonar. CASIZ 081997, one specimen,

United States Fisheries Commission Steamer *Albatross*, ST. D4045, off Kawaihae Light, Hawai'i. Hawai'ian Islands, 269–363 m depth, July 11, 1902. CASIZ 081995, one specimen, United States Fisheries Commission Steamer *Albatross*, ST. D3938, off Laysan Island Light, Hawai'ian Islands, 271–298 m depth, May 16, 1902. CASIZ 081993, one specimen, United States Fisheries Commission Steamer *Albatross*, ST. D3813, off Diamond Head Light, Oah'u. Hawai'ian Islands, 269–363 m depth, March 28, 1902

Distribution: This species is known only from deeper water off Laysan, Oa'hu and Hawai'i in the Hawai'ian Islands.

Etymology: The name *puka*, which is Hawai'ian for *hole*, refers to the large pores on the gizzard plates.

Type locality: Oah'u, Hawai'i.

External morphology: The preserved specimens are uniformly white and about 1 cm in length. The cephalic and posterior shields are approximately equal (Figure 32A). The parapodial lobes are thin, and the posterior notch is deep.

Internal morphology: The shell (Figure 33A) is loosely coiled for a *Philine*, and it has an ovate perimeter. The surface of the shell is smooth.

There is one, short ventral oral gland, and there are two dorsal oral glands. The buccal mass is small, and the radula has the formula $20 \times 1.0.1$ in the two specimens we examined. The broad inner lateral tooth has 39–44 denticles (Figure 33E). There is no crop. The gizzard is muscularized, although the plates are not covered with muscles. The three spindle-shaped plates have large, deep pores (Figure 33C, D). The unpaired plate (Figure 33C) is smaller than the other two (Figure 33D). The plate microsculpture (Figure 33B) consists of regularly arranged polygons, and there is a distinct pattern within each shape. The salivary glands are short.

The nervous system is euthyneurous. The suprainestinal ganglion is adjacent to the fused pleural-parietal ganglion (Figure 32E). The osphradial nerve branches off from halfway between the suprainestinal ganglion and the visceral ganglion. The genital ganglion is distinct.

The penial sac is rectangular, and the penial papilla is hammer-shaped. The base of the papilla is small and has two lobes (Figure 32B). The basal lobe of the hammer is much shorter than the other lobe. The longer lobe is slightly convoluted. The prostate branches (Figure 32C) to the ejaculatory duct, and the posterior end is not connected to the penial sac. The ejaculatory duct is relatively short, and it is not surrounded by the prostate.

The convoluted ampulla narrows (Figure 32D) into

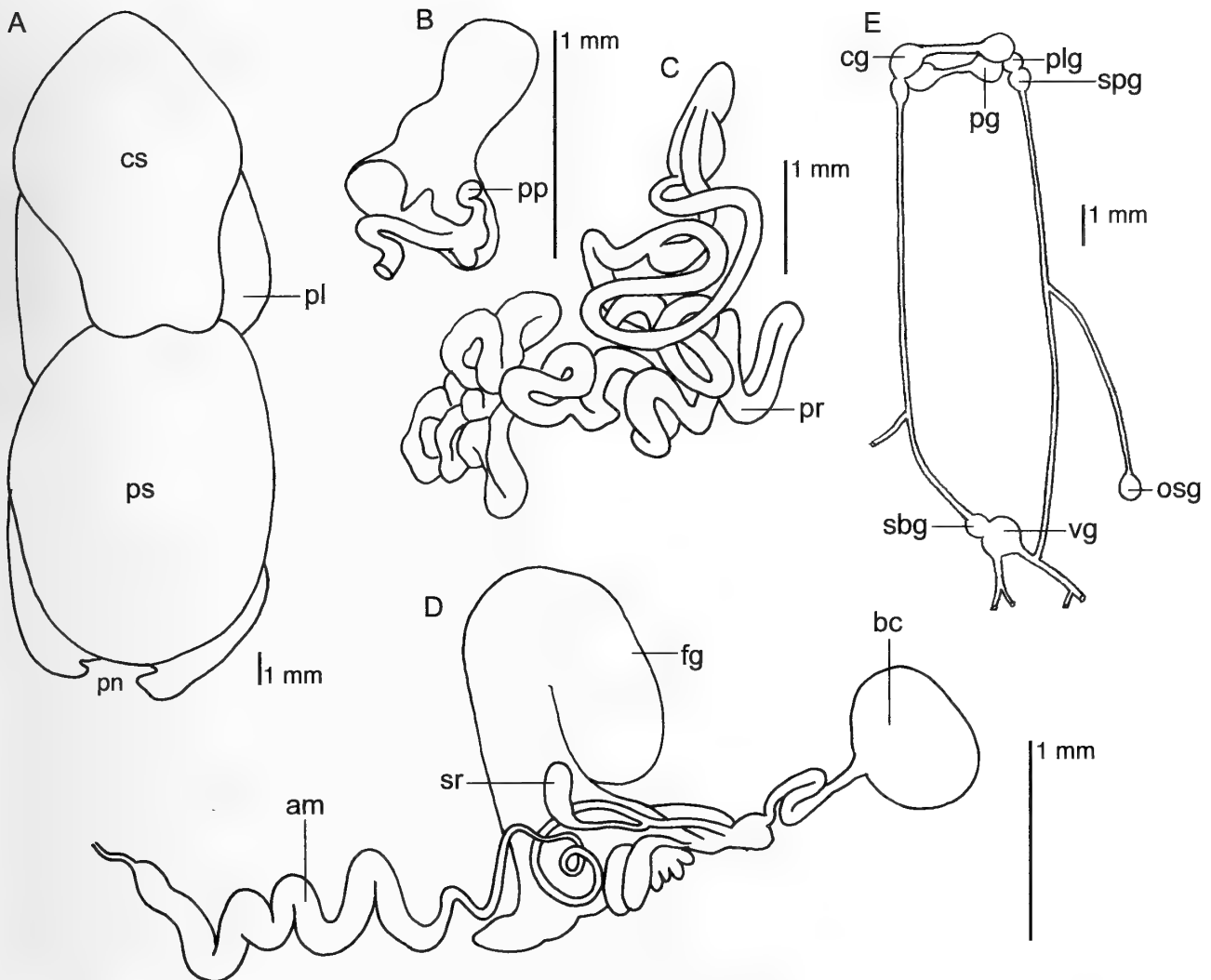


Figure 32. *Philine puka* (CASIZ 082128), anatomy: **A**, dorsal view of a preserved animal; **B**, penis; **C**, male reproductive system; **D**, female reproductive system; **E**, nervous system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **osg**, osphradial ganglion; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pn**, posterior notch; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **spg**, suprainstestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has one lobe above the albumen gland, and the free end bends. The large, rounded bursa copulatrix is situated at the end of the elongate, folded duct. There is a single secondary bursa copulatrix.

Discussion: *Philine puka*, *P. babai* (Valdés, 2008), and *P. habei* (Valdés, 2008) are the only members of the *P. aperta* clade that have been found at depths of at least 200 m.

Philine puka and *P. habei* (Valdés, 2008) are the only two species that have large pores on their gizzard plates, but these two species differ in the

shape of their penial papillae and the dentition of the inner lateral teeth. The hammer-shaped papilla in *P. puka* is narrow with markedly unequal lobes and a reduced base. In *P. habei*, however, the lobes of the hammer-shaped papilla are almost equal in size, and the base is well developed. The inner lateral teeth of *P. habei* lack denticles, whereas those of *P. puka* have 39–44 small denticles.

Philine quadripartita Ascanius, 1772

(Figures 1F, 34, 35)

Philine quadripartita Ascanius, 1772:329, pl. 10, figs. a, b.

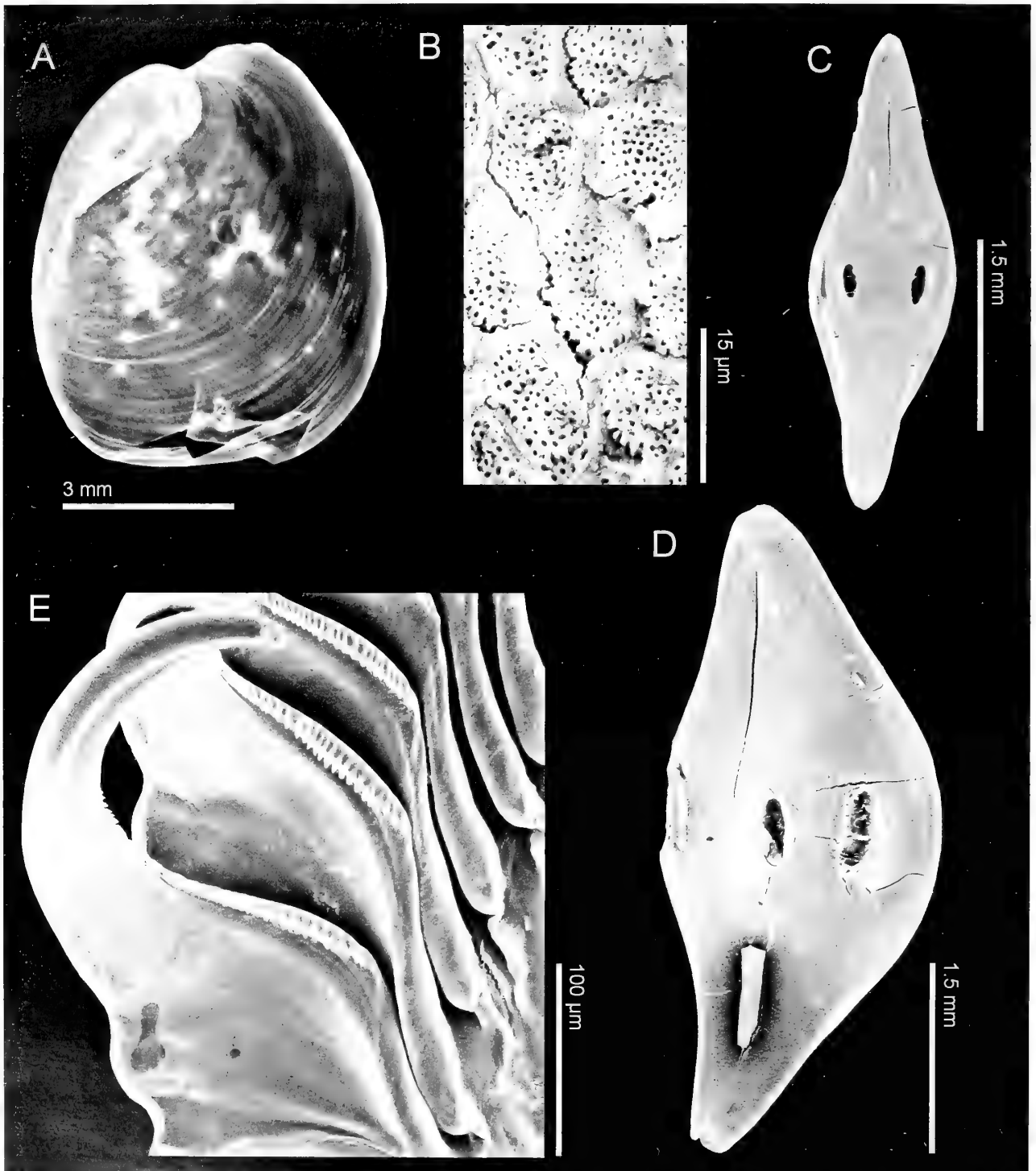


Figure 33. *Philine puka* (CASIZ 082128), photographs of internal hard structures: **A**, light photograph of a ventral view of the shell; **B**, gizzard-plate microstructure; **C**, SEM photograph of the unpaired gizzard plate; **D**, SEM photograph of a paired gizzard plate; **E**, SEM photograph of the radular teeth.

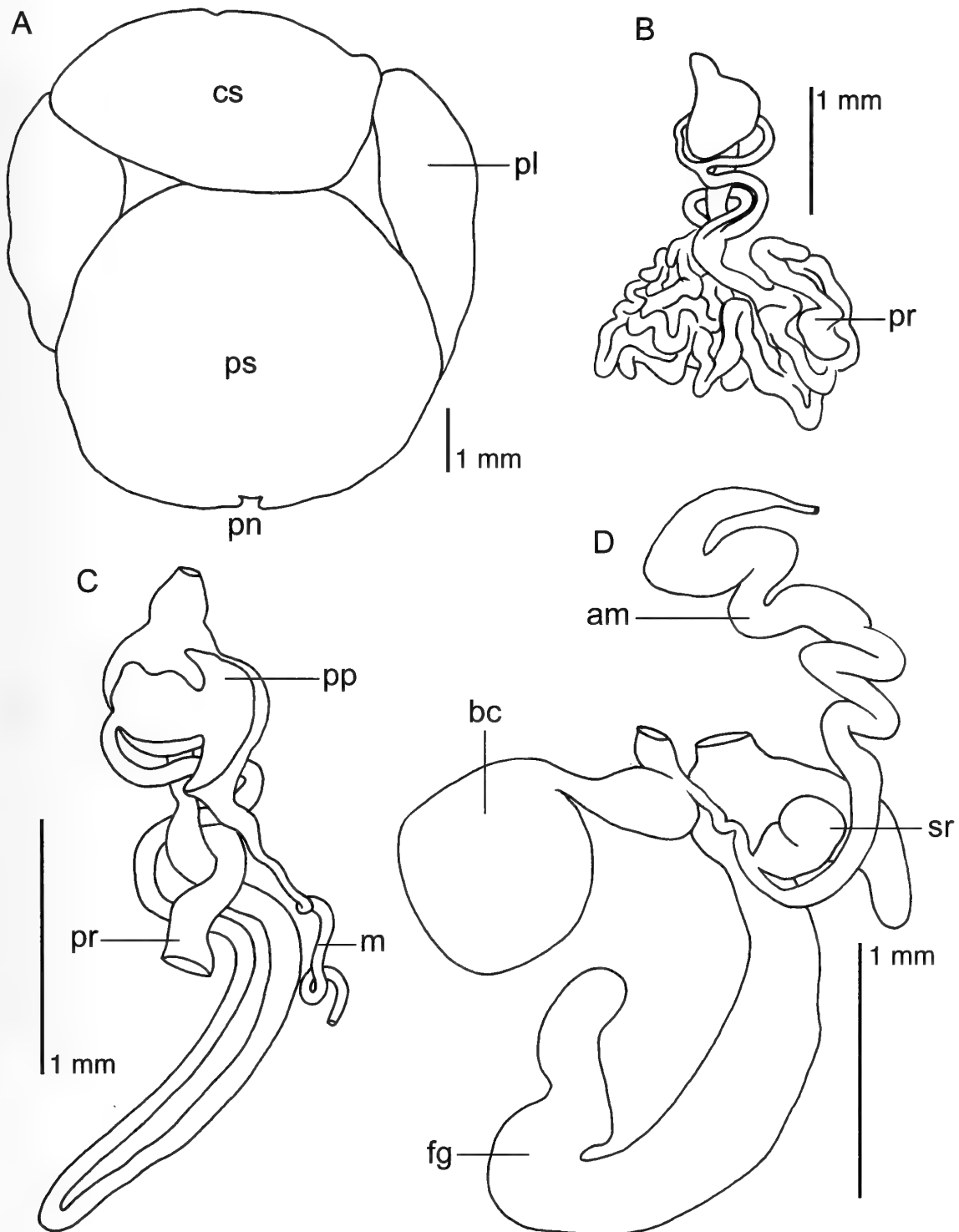


Figure 34. *Philine quadripartita* (CASIZ 066972), anatomy: **A**, dorsal view of a preserved animal; **B**, male reproductive system; **C**, penis and detail of the distal portion of the male reproductive system; **D**, female reproductive system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **fg**, female glands; **m**, muscle; **pl**, parapodial lobe; **pn**, posterior notch; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sr**, receptaculum seminis.

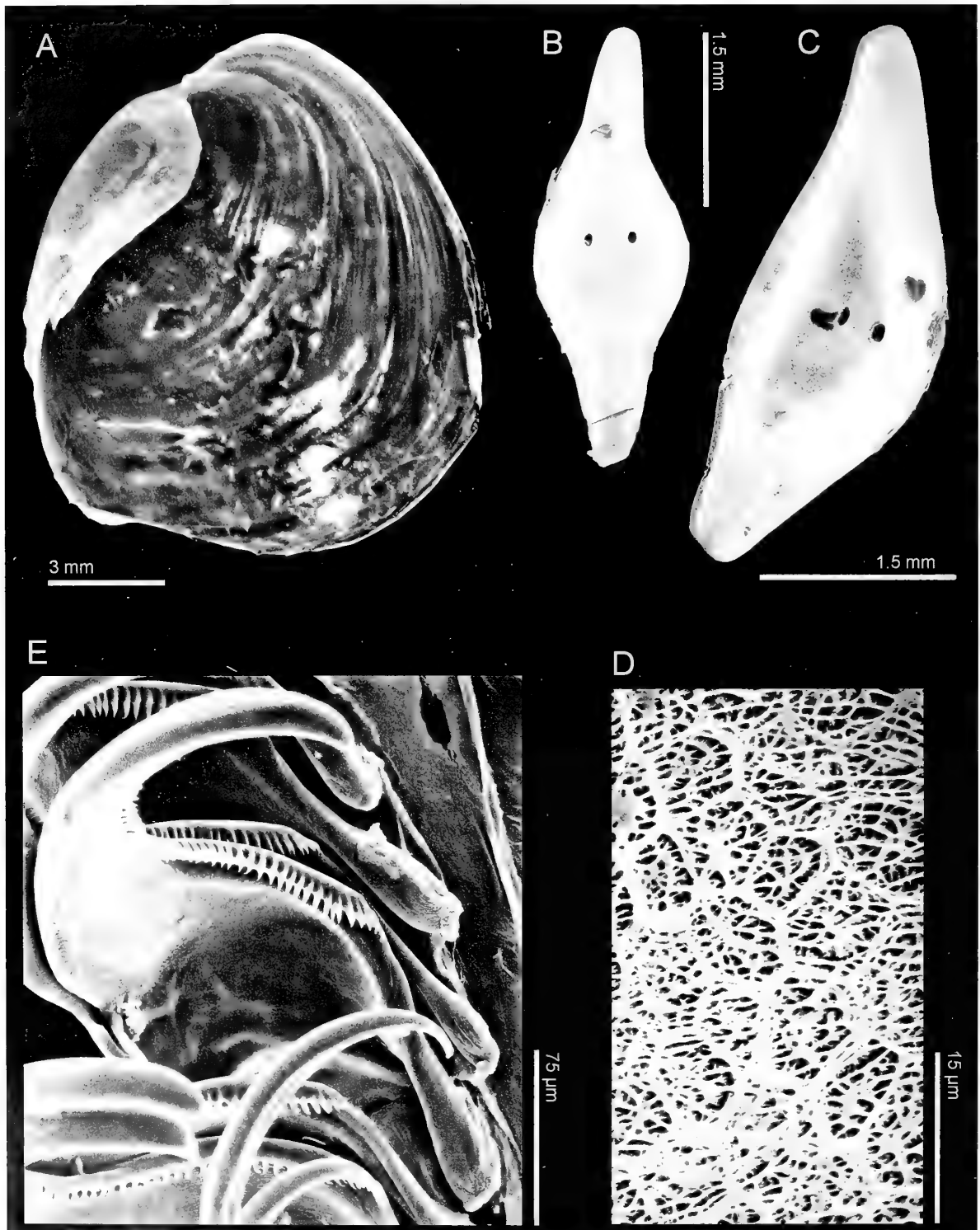


Figure 35. *Philine quadripartita*, photographs of internal hard structures: A, light photograph of a ventral view of the shell (CASIZ 118894); B–E, SEM photographs internal hard structures (CASIZ 066972); B, unpaired gizzard plate; C, paired gizzard plate; D, gizzard-plate microstructure; E, radular teeth.

Lobaria quadriloba Müller, 1776:226.
Lobaria quadrilobata Gmelin, 1791:3143.
Lobaria planciana Lamarck, 1801:63.
Philine aperta var., *patula* Jeffreys, 1867:458.
Philine apertissima deFolin, 1893:147.
Philine milneedwardsi Locard, 1897:35, pl. 1, figs. 7–9.
Philine aperta (Linnaeus) Guiart, 1901:111, figs. 2, 3, 5, 17, 18, 19, 21, 23, 24, 37–42, 50–52, 58–62, 78, 82, 86–88, 99; Brown, 1934:179, figs. 1–38; Thompson, 1976:132, fig. 68, misidentifications.

Material: CASIZ 066972, one specimen, dissected, Naples, Tyrrhenian Sea, Italy, collected by F. M. MacFarland. CASIZ 99117, one specimen, 8 m depth, Cabo Trafalgar, Strait of Gibraltar, Spain, September 27, 1994, T. M. Gosliner. CASIZ 118894, one specimen, outer Swansea Bay, Swansea, Wales, United Kingdom, J. Ellis, March 15, 1993.

Distribution: Known from the British Isles (Thompson, 1976) and throughout the Mediterranean (Cervera et al., 2006).

External morphology: The living animal (Figure 2F) is white and ranges in size from approximately 1 to 3 cm. The cephalic shield is longer than the posterior one (Figure 34A). The parapodial lobes are thick and muscular, and the posterior notch is deep.

Internal morphology: The shell (Figure 35A) is open with an ovate perimeter. Punctate microsculpture is absent, and the surface of the shell is smooth.

There are two dorsal oral glands, and a single, short ventral oral gland. The buccal mass is small. The radular formula is $16-19 \times 1.0.1$, and the broad inner lateral teeth have between 43 and 52 denticles (Figure 35E). The crop is indistinct and, although the gizzard is muscularized, muscles do not cover the three large gizzard plates. The gizzard plates are spindle-shaped with two medium-sized pores (Figure 35B, C). The unpaired plate (Figure 35B) is smaller than the other two. The microsculpture (Figure 35D) consists of regularly arranged polygons. The structure within each polygon is disorganized. The salivary glands are short.

The suprainestinal ganglion is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off from halfway between the suprainestinal ganglion and the visceral ganglion. The genital ganglion is fused to the visceral one, which is, in turn, fused to the subintestinal ganglion.

The penial sac is ovate, and the penial papilla is hammer-shaped (Figure 34B, C). The hammer handle is a simple stalk. The lobes of the hammer head are subequal. One lobe protrudes over the prostate, stretching the shape of the penial sac. The prostate branches to the ejaculatory duct, and the posterior end is connected to the penial sac by a long muscle. The

prostate is composed of a distinct aggregation of glandular cells. The ejaculatory duct is short and surrounded by much of the prostate.

The convoluted ampulla narrows (Figure 34D) into the hermaphroditic duct, at the side of which branches a single, long, and narrow receptaculum seminis. The bursa copulatrix is large with a short, thick stalk, and there is a single secondary bursa copulatrix.

Discussion: *Philine quadripartita* is the most extensively studied species in this genus, and there are detailed descriptions of the anatomy and developmental biology (Brown, 1934) and diet (Hurst, 1965), perhaps because its distribution includes the Mediterranean and the British Isles, areas in which the fauna is well known. However, most subsequent authors followed the convention of Lemche and others and considered their material to be *P. aperta*.

Philine quadripartita and *P. aperta* are very similar in their morphology, and they have often been considered synonymous. However, we found consistent differences that justify separating the two species. First, the gizzard plates of *P. quadripartita* are proportionately smaller and narrower, whereas the paired plates of *P. aperta* are broad, even approximating circularity in one drawing by Marcus & Marcus (1966:fig. 9). Second, the gizzard-plate microsculpture of the two species is different. In *P. quadripartita*, the microsculpture consists of flat polygons within which there is no obvious pattern. In *P. aperta*, however, the polygons are indented, more circular, and contain a regular subsulpture. Third, the penial papilla in *P. quadripartita* is smaller, and the knob on the penial stalk is less pronounced. Fourth, the penial papilla of *P. quadripartita* extends in a pointed extension of the penial sack, whereas in *P. aperta* the entire papilla is contained in a rounded sac. Finally, the egg mass is globular in *P. quadripartita* (Guiart, 1901:fig. 16; Rudman, 1998c) and elongate and tubular in *P. aperta* (Figure 2B).

Philine sarcophaga Price, Gosliner, and Valdés,
 sp. nov.

(Figures 36, 37)

Type material: Holotype: SAM, Meiring Naude Cruise, Station SM 67, specimen 22 mm, coarse sand, 680–700 m depth, 27°14.8'S, 32°54.6'E, May 20, 1976. Paratypes, CASIZ 175006, Meiring Naude Cruise, Station SM 67, two specimens, 15–18 mm, one dissected, coarse sand, 680–700 m depth, 27°14.8'S, 32°54.6'E, May 20, 1976.

Distribution: Known only from the tropical KwaZulu Natal coast of South Africa.

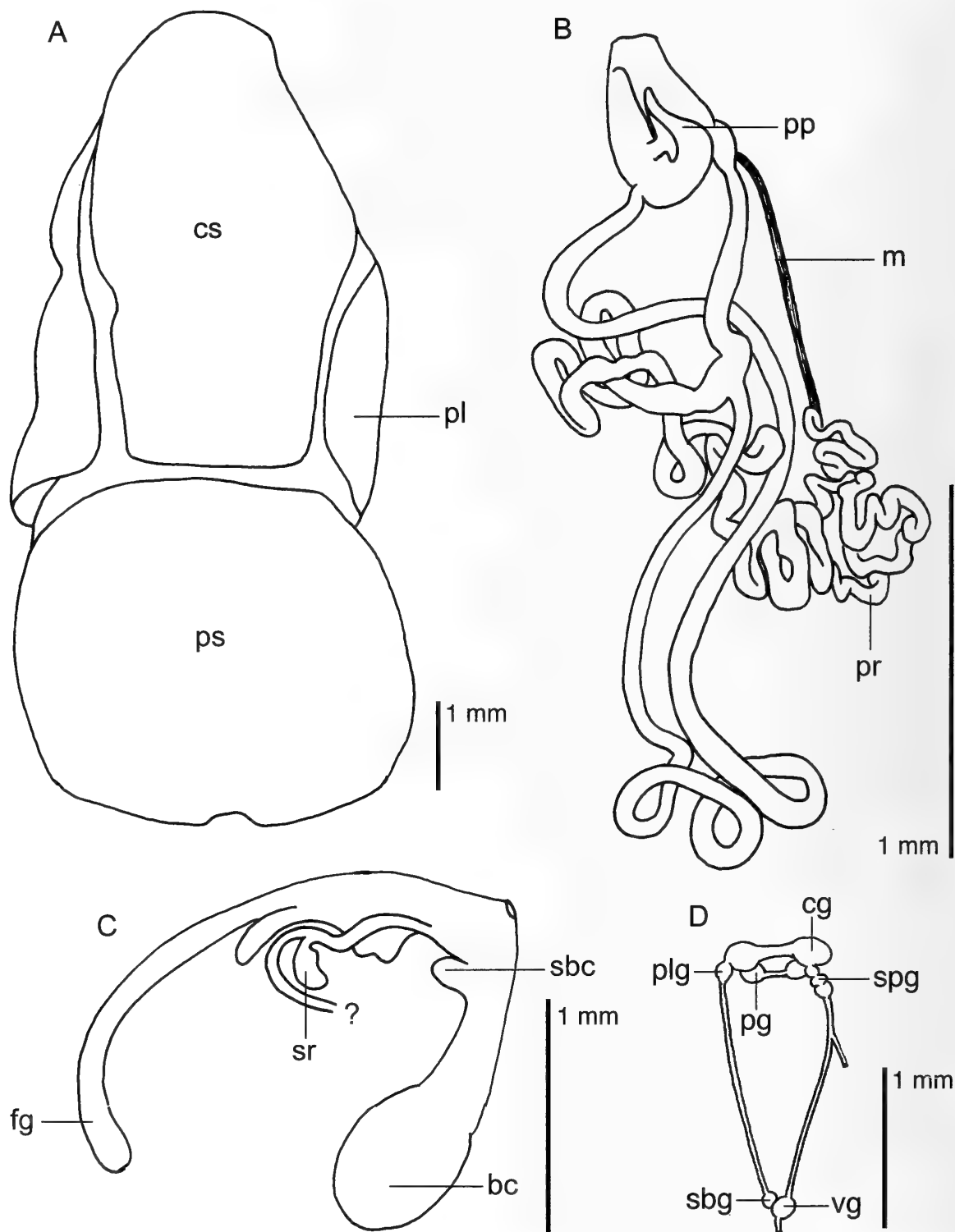


Figure 36. *Philine sarcophaga* (CASIZ 175006), anatomy: **A**, dorsal view of a preserved animal; **B**, male reproductive system; **C**, female reproductive system; **D**, nervous system. Abbreviations: **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **m**, muscle; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sbg**, subintestinal ganglion; **spg**, suprainstestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

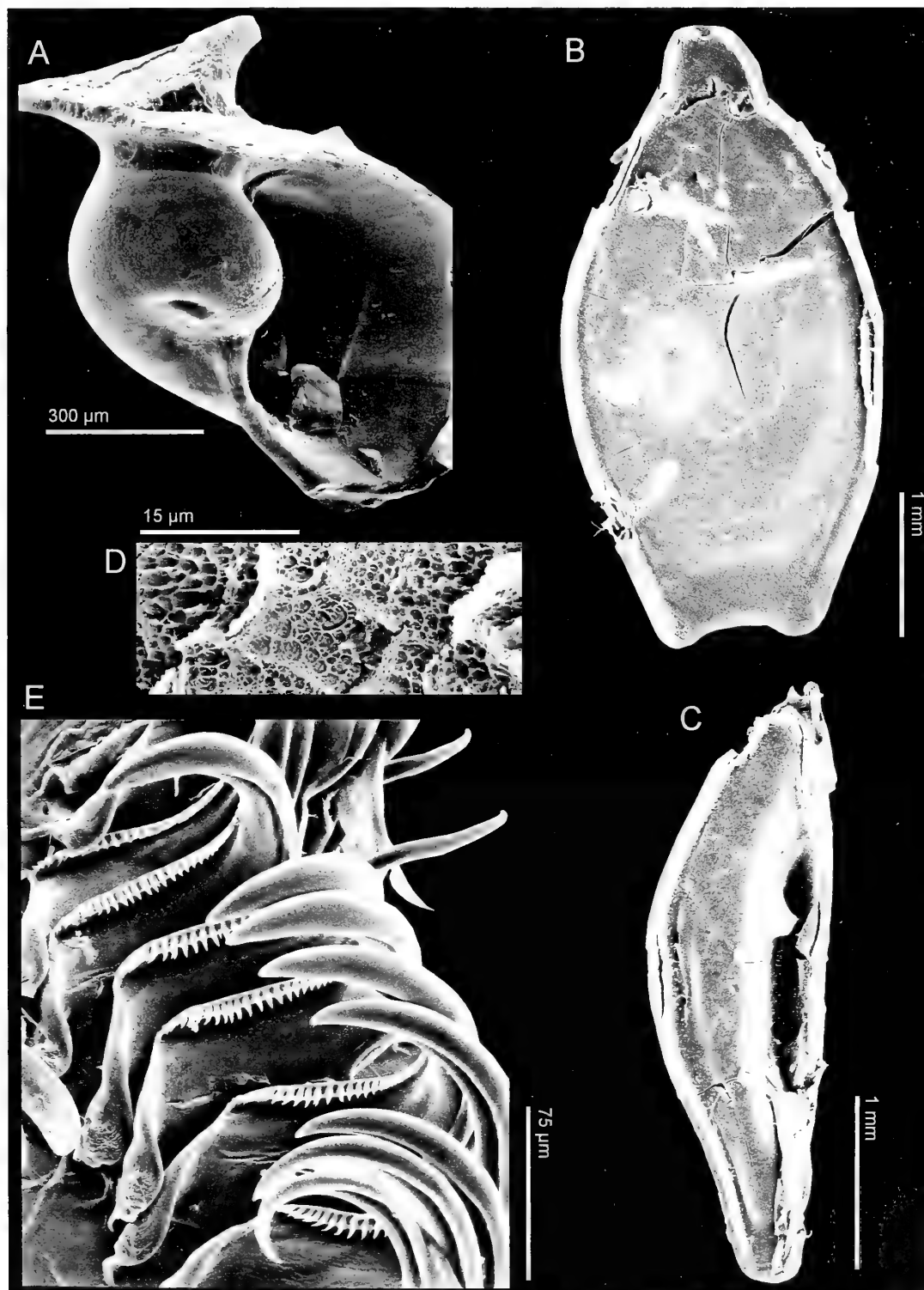


Figure 37. *Philine sarcophaga* (CASIZ 175006), SEM photographs of internal hard structures: **A**, protoconch; **B**, unpaired gizzard plate; **C**, paired gizzard plate; **D**, gizzard-plate microsculpture; **E**, radular teeth.

Etymology: The specific epithet, *sarcophaga*, refers to the coffin-shaped, unpaired gizzard plate.

Type locality: Kwazulu Natal, South Africa.

External morphology: The preserved specimens are white and vary in size from approximately 10 to 12 mm. The cephalic shield is longer than the posterior one (Figure 36A). The parapodial lobes are thin, and the posterior notch is shallow.

Internal morphology: The punctate shell (Figure 37A) is relatively tightly coiled for a *Philine*.

There are two dorsal oral glands and one ventral oral gland. The buccal bulb is reduced, and the radular formula is $18-19 \times 1.1.0.1.1$ (Figure 37E). The inner lateral teeth are broad with 18–31 small denticles. The outer laterals are thin and elongate, without denticles. The gizzard is muscularized and covers the two smaller plates but not the larger unpaired plate. The gizzard lacks a distinct crop posterior to the plates. The two paired plates are spindle-shaped with long slits on the flatter side (Figure 37C). The unpaired plate is much larger than the others and more rhomboidal (Figure 37B); its anterior end is rounded, and its posterior end is concave; it lacks slits, and it is larger than the other two plates. The plate microsculpture (Figure 37D) consists of a meshwork of polygons. The salivary glands are short.

The nervous system (Figure 36D) is eutyneurous. The fused pleural-parietal ganglion is adjacent to the anterior suprainestinal ganglion. The visceral ganglion is fused to the subintestinal ganglion. It is not known whether the genital ganglion is fused to the visceral ganglion.

The penial papilla (Figure 36B) is hammer-shaped, and the lobes of the hammer head are markedly unequal. The papilla rests in the penial sac. The elongated prostate branches to the ejaculatory duct, which is long and not covered by the prostate.

The ampulla (Figure 36C) narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has one lobe but may be fully mature. The bursa copulatrix is large and rounded with a thick, elongate duct. There is one secondary bursa copulatrix.

Discussion: The paired gizzard plates are similar to those in *P. infundibulum*, in that they are flat on one edge and curved on the other edge. The plates in *P. sarcophaga* have two slits, with the slit along the long edge being much larger than the other. However, *P. infundibulum* has only one slit, which may be homologous to the larger slit in *P. sarcophaga*. The unpaired plates in both species are symmetrical, although, in *P. sarcophaga*, the anterior end is rounded and extended and the posterior end is concave, whereas in *P. infundibulum* both ends are simply rounded.

The penial papilla of *P. sarcophaga* is quite different from that of *P. infundibulum*. Instead, it is more similar to that of *P. orientalis*. The hammer-shaped tip of the papilla is small with markedly subequal lobes, but it is appressed with a fat base, and an additional large lobe swings up and around from the base, terminating in a point.

Another species described from South Africa is *Philine berghi* Smith, 1910. This species originally was misidentified as *P. capensis* by Bergh (1907). *Philine capensis* Bergh, 1907, was shown to be a junior homonym of *B. capensis*, which has been shown to be a junior synonym of *P. aperta* (Smith, 1910). Based on this fact, Smith erected a new name, *P. berghi*, for the species described in Bergh's article. O'Donoghue (1929) also referred to *P. berghi*. As in *P. sarcophaga*, *P. berghi* has a large rhomboidal gizzard plate without pores (Bergh, 1907:pl. 5, fig. 15), but *P. berghi* has two rows of outer lateral teeth, as opposed to the single row found in *P. sarcophaga*. In addition, the medial plate of *P. berghi* is somewhat smaller than the two lateral plates (described but not illustrated by Bergh), whereas in *P. sarcophaga* the medial (unpaired) plate is much larger than the lateral plates. No additional material matching Bergh's description has been found in any of the material housed in the collections of the South African Museum. Further distinctions must await the discovery of additional material matching Bergh's description.

Philine thurmanni thurmanni Marcus and Marcus
1969

Philine thurmanni thurmanni Marcus and Marcus,
1969:14–17, figs. 23–28.

Distribution: South Atlantic Ocean off the coast of Argentina.

External morphology: The living animal is white and varies between 2 and 9.5 mm. The cephalic shield is shorter than the posterior shield.

Internal morphology: The shell, which has prominent punctate sculpture, is ovate and only slightly coiled.

The buccal bulb is reduced, and the radula has formula $14-16 \times 1.1.0.1.1$. The inner lateral teeth are broad with an unspecified number of small denticles. The gizzard is muscularized and surrounded by three large, equal-sized plates. The plates lack any pores or slits. The gizzard lacks a distinct crop.

The penial papilla is hammer-shaped, and the lobes of the hammer head are markedly unequal. The papilla rests in the penial sac. The elongated prostate branches to the ejaculatory duct.

Discussion: The summary above is based on the original

description in Marcus & Marcus (1969) and Marcus (1974). These descriptions are sufficiently complete to identify the species in the *aperta* complex, so we did not deem it necessary to analyze additional material. Because Marcus & Marcus (1969) and Marcus (1974) did not describe the nervous system or female reproductive anatomy, many of the character states for this species are missing from our matrix. Still, the branched ejaculatory duct, the hammer-shaped penial papilla, and the spindle-shaped gizzard plates place this species within the *P. aperta* clade.

PHYLOGENETIC ANALYSIS

Despite the description of more than 100 species of *Philine* and the erection of many different genera (including *Hermania* Monterosato, 1884; *Laona* A. Adams, 1865; *Philinorbis* Habe, 1950; *Yokoyamaia* Habe, 1950; *Globophilina* Habe, 1958; and *Spiniphiline* Gosliner, 1988), no study has been undertaken to construct a phylogenetic hypothesis of the group or to test the monophyly of any of these genera. We present an initial phylogeny of *Philine* species, including two outgroup taxa and 26 ingroup taxa that span much of the variability of the genus based on the analysis of 46 morphological characters.

Morphological Variability and Character Polarity

We have included 46 characters to determine phylogenetic relationships within the genus. Polarity was determined by using *C. alba* and *S. mundus*, two presumed close relatives of *Philine*, as outgroups. Twenty-six ingroup taxa were included in the analysis. Character polarities were determined using outgroup comparison in the phylogenetic analysis. The character matrix is presented in Table 2. All multistate characters are treated as unordered. The following characters and states were used.

Body

1. **Animal color:** The outgroup species and most *Philine* species are uniformly white in their body color. The known exceptions are *Philine caledonica* Risbec, 1951; *Philine rubra* Bergh, 1905; *Philine rubrata* Gosliner, 1988 (fig. 2H), and *Philine orca* Gosliner, 1988 (fig. 2G). 0: white; 1: not white.
2. **Ratio of cephalic shield to posterior shield:** Both in *Cylichna* and *Scaphander*, the cephalic shield is shorter than the posterior shield. This arrangement is plesiomorphic in *Philine*, but some species have cephalic shields that are the same length as the posterior shield, and others have cephalic shields that are even longer than the length of the

posterior shield. This character is difficult to code in animals that were not relaxed before being preserved, because the manner in which the mantle contracts dictates body shape. In all cases, this character was determined from photographs of living animals or from preserved specimens that are well extended. 0, short cephalic shield; 1, long cephalic shield; 2, cephalic and posterior shields equal.

3. **Parapodial lobes:** Parapodial lobes span the sides of the cephalic shield. They are plesiomorphically weak and flimsy, but they can be muscular, as in *P. aperta*, *P. orientalis*, and *P. quadripartita*. 0, narrow; 1, thick.
4. **Posterior notch:** The posterior end of the posterior shield can be rounded or notched. A notch, even if actually present, is not always evident in all preserved specimens. Thus, it was necessary to examine multiple specimens to code this character effectively. In species, such as *P. aperta* and *P. sarcophaga*, the posterior notch is shallow. In species such as *P. auriformis*, the posterior notch is deep. 0, absent; 1, shallow; 2, deep.
5. **Elongate skirt:** In *Philine pruinosa* and *P. rubrata*, an elongate skirt wraps around the posterior shield and opens at the posterior end. This character is illustrated elsewhere (Gosliner, 1988:fig. 4). It applies only to species with a robust mantle that covers the shell, and thus cannot be coded for *Philine lima* and *P. t. thurmanni*, whose shells are covered by only a thin membrane. 0, absent; 1, present.
6. **Mantle cavity:** The mantle cavity is located on the right side of *Scaphander* and *Cylichna*, but it is located at the posterior end of the animal in all *Philine* species. We used this character to distinguish the ingroup from the outgroup. 0, right; 1, posterior.

Shell

7. **Shell:** *Scaphander mundus* and *C. alba* have external shells, whereas all *Philine* species have internal shells. This character differentiates *Scaphander* and *Cylichna* from the ingroup. 0, external; 1, internal.
8. **Shell sculpture:** *Scaphander mundus* and the more basal members of *Philine* have punctate shells. Other authors describe this punctuation as "catenoid" (e.g., Lemche, 1948) or spiral sculpture (e.g., Marcus & Marcus, 1969). Our observations suggest that juveniles are usually punctate, but that, in some species, the adults deposit an additional, smooth layer over the punctations. Only adult shells were used to code this character. 0, punctate; 1, smooth.

Table 2
Character matrix of *Philine* and outgroups

	<i>alba</i>	<i>alboides</i>	<i>angasi</i>	<i>aperta</i>	<i>aurifor-</i> <i>mis</i>	<i>babai</i>	<i>berghi</i>	<i>elegans</i>	<i>falklan-</i> <i>dica</i>	<i>fenestra</i>	<i>finmarch-</i> <i>ica</i>	<i>gibba</i>	<i>habei</i>
1	0	0	0	0	0	0	?	0	0	0	0	0	0
2	1	0	1	1	1	2	?	2	0	1	2	0	1
3	0	0	0	1	0	0	?	0	0	0	0	0	0
4	0	0	0	1	2	0	?	2	1	0	1	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	1	1	1	1	1	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1	1	1	1	1
8	1	1	1	1	0	0	?	1	1	0	1	1	1
9	1	1	1	1	1	1	?	?	0	1	0	1	1
10	0	0	1	0	0	2	?	0	0	0	0	0	2
11	0	0	2	1	1	2	?	1	2	1	1	2	2
12	0	0	1	1	?	1	?	1	0	1	1	0	1
13	0	0	1	1	1	1	?	1	0	1	1	0	1
14	1	2	2	2	2	2	2	2	1	2	2	1	2
15	1	1	3	3	2	2	1	3	1	2	3	1	3
16	0	0	0	0	0	0	?	0	0	0	0	0	3
17	0	0	0	0	0	0	?	0	0	0	0	0	0
18	0	0	1	1	1	1	?	1	0	1	1	0	1
19	1	1	0	0	0	0	?	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	1	1	1	1	1	1	0	1	1	0	1
22	0	0	1	1	1	1	?	1	0	1	1	1	1
23	0	0	1	1	1	1	?	1	0	1	1	0	1
24	0	0	0	0	0	2	?	1	0	0	0	0	0
25	0	0	1	1	?	0	?	1	?	1	?	?	1
26	0	0	1	0	0	1	?	1	0	0	0	0	0
27	0	0	1	1	0	1	1	1	?	1	0	?	1
28	0	0	2	2	0	2	2	2	0	0	0	0	2
29	NA	NA	0	0	NA	1	?	1	?	0	NA	?	0
30	0	0	2	2	0	0	0	2	0	0	0	0	2
31	?	?	1	1	?	?	?	1	?	?	?	?	2
32	0	0	0	0	2	2	?	0	0	2	0	0	0
33	0	0	1	1	1	1	?	1	0	1	1	0	1
34	0	0	2	2	2	2	?	2	0	2	2	0	2
35	NA	NA	0	0	0	0	?	1	NA	1	0	NA	1
36	?	?	0	0	0	1	?	0	?	0	0	?	1
37	0	0	1	1	1	1	?	1	0	1	1	0	1
38	?	?	1	0	0	1	?	0	?	0	?	?	0
39	?	?	0	1	1	0	?	0	?	1	?	?	1
40	0	0	0	0	0	0	?	0	0	0	0	1	0
41	0	0	0	0	0	0	?	0	1	0	0	0	0
42	0	0	0	0	0	0	?	0	0	0	1	1	0
43	1	1	1	1	1	1	?	1	0	2	0	0	1
44	1	1	1	1	1	1	1	1	1	1	1	1	1
45	0	0	2	2	2	2	?	2	0	2	2	1	2
46	1	1	1	1	1	1	?	1	1	?	1	0	1

The character states are indicated with numbers, 0: plesiomorphic condition, 1-2: apomorphic conditions. Question marks indicate unknown data. NA indicates non-applicable characters.

9. **Shell coiling:** The shells of *Scaphander* and *Cylichna* are more tightly coiled (i.e., their shells have more whorls or a lower expansion rate) than the shells in most *Philine* spp., Thus, *Philine* shells have a higher whorl expansion rate (following the terminology in Raup, 1961). A high whorl expansion rate means that the posterior shield is

broad and disc-shaped. 0, tightly coiled; 1, high whorl expansion rate.

Digestive System

10. **Ventral oral glands:** The number of ventral oral glands in *Philine* varies between one and two. We

Table 2
Extended

<i>infundibulum</i>	<i>lima</i>	<i>orca</i>	<i>orientalis</i>	<i>paucipapillata</i>	<i>pruinosa</i>	<i>puka</i>	<i>quadrata</i>	<i>quadrupartita</i>	<i>rubrata</i>	<i>sarcophaga</i>	<i>thurmanni</i>	<i>Spiniphiline kensleyi</i>	<i>Cylichna alba</i>	<i>Scaphander mundus</i>
0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
1	1	0	1	1	2	2	2	1	0	1	0	1	0	0
0	0	0	1	1	0	0	0	1	0	0	?	0	0	0
?	0	1	0	2	2	2	1	2	2	1	?	2	0	0
0	?	0	0	0	1	0	0	0	1	0	?	0	?	?
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
1	0	0	0	1	0	1	0	1	0	1	0	1	1	0
1	0	1	1	1	0	1	1	1	1	1	0	0	0	0
0	?	1	1	1	?	0	?	0	0	0	?	1	?	?
1	?	1	2	1	?	1	?	1	1	1	?	0	?	?
1	?	1	1	1	?	1	0	1	1	1	?	1	0	0
1	1	1	1	1	?	1	1	1	1	1	?	0	0	0
2	2	2	2	2	2	2	2	2	2	2	2	2	0	1
2	1	1	3	3	0	3	1	3	1	2	2	2	0	3
0	3	2	0	0	0	0	0	0	1	0	0	0	0	0
0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	1	1	?	1	1	1	0	1	1	0	0	0
0	1	1	0	0	?	0	?	0	0	0	0	0	0	0
0	1	1	0	0	1	0	1	0	2	0	0	0	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	1	0	2
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	1	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	1	1	0	1
0	NA	NA	NA	NA	NA	NA	NA	0	NA	0	0	0	0	0
0	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	?	?	?
0	NA	NA	NA	NA	NA	NA	NA	0	NA	0	0	0	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	0	1	0	0
1	NA	NA	NA	NA	NA	NA	NA	2	NA	1	0	2	0	2
1	NA	NA	NA	NA	NA	NA	NA	0	NA	1	NA	?	NA	NA
0	NA	NA	NA	NA	NA	NA	NA	2	NA	0	0	0	0	0
?	NA	NA	NA	NA	NA	NA	NA	1	NA	?	?	?	?	?
1	NA	NA	NA	NA	NA	NA	NA	0	NA	2	0	0	0	0
1	0	0	1	1	?	1	0	1	0	1	1	0	0	0
2	3	0	2	2	?	2	0	2	0	2	2	0	0	0
0	NA	NA	0	1	NA	1	NA	0	NA	1	1	NA	NA	NA
0	?	?	0	0	?	1	?	1	?	0	0	?	?	?
1	0	0	1	1	?	1	0	1	0	1	1	0	0	0
1	?	?	1	0	?	0	?	0	?	1	?	?	?	?
1	?	?	0	1	?	1	?	1	?	0	?	?	?	?
0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
0	0	1	0	0	?	0	0	0	0	0	0	0	0	0
0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
1	0	0	1	1	?	1	0	1	0	1	?	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
2	1	2	2	2	?	2	1	2	2	2	?	2	1	0
1	0	1	1	1	?	1	0	1	1	1	?	1	1	1

do not know how many ventral oral glands *C. alba* and *S. mundus* have. 0, one; 1, two; 2, absent.

11. **Dorsal oral glands:** *Philine* species have zero, one, or two dorsal oral glands. We do not know how many dorsal oral glands *C. alba* and *S. mundus* have. 0, one; 1, two; 2, zero.
12. **Salivary glands:** The salivary glands may be longer than the buccal mass, as in *P. alba* and *P. alboides*, or they may be short and stubby, as in the

members of the *P. aperta* clade, where they are much shorter than the buccal mass. 0, long; 1, short.

13. **Size of radula relative to body:** The outgroup taxa and the basal members of *Philine* have a larger radula than the species of the *Philine aperta* clade. 0, large; 1, reduced.
14. **Rachidian tooth:** The rachidian tooth is only present in the outgroup and in such basal members of *Philine* as *Philine gibba* and *Philine falklandica*.

- It may be vestigial or absent in *P. alba*. When present in *Philine*, the rachidian tooth is small and may be vestigial. 0, large; 1, small; 2, absent.
15. **Number of outer lateral teeth:** *Cylichna alba* and *S. mundus* have many lateral teeth, as does *P. pruinosa* (Thompson, 1976). As shown by Gosliner (1994:279), opisthobranch outer teeth are not homologous with the marginal teeth found in Vetigastropoda and are therefore referred to as outer lateral rather than marginal teeth. Some basal members of *Philine* have two outer lateral teeth. Within the *P. aperta* clade, species have either one outer lateral (e.g., *P. sarcophaga*) or none (e.g., *P. orientalis*). 0, many teeth; 1, two teeth; 2, one tooth; 3, no teeth.
 16. **Inner lateral denticles:** Although inner lateral denticles are absent in *P. lima* (Lemche, 1948) and *P. habei* (Valdés, 2008), most species have 30–80 minute denticles. *Philine rubrata* is autapomorphic for having 10–11 elongate denticles, and *P. orca* is autapomorphic for one large denticle (Gosliner, 1988). 0, several small; 1, some medium; 2, one large; 3, absent.
 17. **Width of inner lateral ridge:** Most inner lateral teeth have a broad ridge on which the denticles are located, whereas *P. lima* and *P. pruinosa* have a narrow ridge. 0, broad; 1, narrow.
 18. **Crop:** Some species have a distinct crop above the gizzard, whereas others lack the crop entirely. *Philine infundibulum* has a widening of the esophagus below the gizzard, but this area does not seem to be homologous with the crop as it has a different structure. 0, distinct; 1, indistinct.
 19. **Muscularized gizzard:** *Philine alba* and *P. alboides* have virtually no muscularization of the gizzard and are therefore similar to the Aglajidae. All other *Philine* that have a gizzard that is muscularized. 0, muscularized; 1, not muscularized.
 20. **Plates present:** The plesiomorphic condition for *Philine* is to have three prominent gizzard plates, as in the outgroup taxa. Some species, such as *P. rubrata* (Gosliner, 1988), have plates that are reduced to chitinous ridges within a muscular region of the esophagus and are considered vestigial, and some species have no plates at all. Some authors have observed reduced plates in *P. quadrata*, but others claim that *P. quadrata* lacks plates entirely (Thompson, 1976; present study). We infer that, when *P. quadrata* plates are present, they must be vestigial. 0, three plates present; 1, vestigial; 2, absent.
 21. **Shape of gizzard plates:** *Cylichna*, *Scaphander*, and some *Philine* species have gizzard plates that look like kidney beans. *Scaphander* has similarly shaped plates, but they are tiered so that a notch between the layers is visible in profile. Members of the *P. aperta* clade have spindle-shaped plates. The spindle may be somewhat triangular. 0, kidney-bean shaped; 1, spindle-shaped; 2, tiered.
 22. **Esophagus goes through plates:** In some species, the gizzard lacks definition within the plates and no distinct esophageal duct is observed within the gizzard. In other species, the esophagus is clearly present as a distinct tube that passes through the gizzard. 0, without definition; 1, distinct tube.
 23. **Plate size relative to body size:** Some *Philine* species have small plates, whereas others have large ones. This refers to species that have three plates in character 20, and it refers to the size of these plates. 0, small; 1, large.
 24. **Plate margin:** Most *Philine* species have plates with a smooth margin. *Philine elegans* is autapomorphic for a fringed plate, and *P. babai* (Valdés, 2008) is autapomorphic for irregular crenulations. 0, smooth; 1, fringed; 2, irregular.
 25. **Texture in plate microstructure:** Fine microstructure of the exterior (rather than esophageal) side of the plates arranged as a series of irregularly shaped polygons may be apparent when the gizzard plates are observed under SEM at the micrometer scale. Both outgroup taxa lack microsculpture. 0, absent; 1, present.
 26. **Twisted plates:** The paired plates in *P. angasi*, *P. elegans*, and *P. babai* Valdés, 2008, have an S-like twist along the long axis. 0, absent; 1, present.
 27. **Two plates that are paired:** Some *Philine* species have equal-sized plates, as does *Cylichna*. In other species, however, there are two paired plates that are mirror images of each other. 0, paired plates absent; 1, paired plates present.
 28. **Sizes of unpaired plates:** *Philine* species can have two paired plates of the same size, an unpaired plate that is smaller than the paired plates, or an unpaired plate that is larger than the paired plates. 0, equal; 1, unpaired plate is larger; 2, unpaired plate is smaller.
 29. **Shapes of unpaired plates:** When one of the gizzard plates differs from the other two plates, it may be spindle-shaped, as in *P. aperta*, or rhomboidal, as in *P. elegans*. This character describes the shape of the unpaired plate, and it is therefore not applicable to any taxa that do not have paired plates. 0, spindle; 1, rhomboidal.
 30. **Plate pores:** Some of the gizzard plates have pores on their outer surface. 0, pores absent; 1, pores present.
 31. **Pore size:** Pores on the gizzard plate can be small (*P. paucipapillata*; Figure 31B, C), medium (*P. aperta*; Figure 3A, B), or large (*P. puka*; Figure 33C, D). 0, small; 1, medium; 2, large.
 32. **Slits on paired plates:** *Philine infundibulum* has one long slit on each of its paired plates. *P. babai*

(Valdés, 2008) and *P. sarcophaga* have two long slits on their paired plates. *Philine auriformis* and *P. fenestra* also have two long slits, but these slits are present on all three, equal-sized gizzard plates. 0, absent; 1, one long slit; 2, two long slits.

Reproductive System

33. **Relative length of the prostate:** Several members of *Philine* are characterized by a long and convoluted prostate that often extends beyond the length of the gizzard *in situ*, whereas other members have a short, simple prostate. 0, short and straight; 1, convoluted and elongate.
34. **Shape of penial papilla:** The penial papilla may be a simple cone, a bilobed point, or hammer-shaped. Sometimes the papilla is completely absent, as in *P. lima* (Lemche, 1948; Marcus & Marcus, 1969). 0, simple conical; 1, bilobed; 2, hammer; 3, absent.
35. **Hammer head lobes:** When the penial papilla is hammer-shaped, the lobes on the hammer "head" may be approximately the same size, or one lobe may be much larger than the other. 0, subequal; 1, markedly unequal.
36. **Penial papilla sac:** The base of a hammer-shaped penial papilla may fit within the penial sac or it may distend the sac. This character does not seem to vary within species and is therefore not likely a preservational artifact. 0, contained within sac; 1, distends the sac.
37. **Ejaculatory duct is a specialized branch of the prostate:** The ejaculatory duct may form a separate branch of the convoluted and elongate prostate. 0, absent; 1, present.
38. **Length of the ejaculatory duct:** The ejaculatory duct may be long, extending far below the prostate, as in *P. orientalis* (Figure 26B), or it may be short, as in *P. aperta* (Figure 3C). 0, short; 1, extends far beyond prostate.
39. **Ejaculatory duct surrounded by prostate:** The ejaculatory duct may be surrounded by the rest of the prostate (*P. angasi*), or it may be adjacent to the prostate (*P. aperta*). 0, naked; 1, covered.
40. **Spermatic bulb:** The simple prostate in *P. gibba* terminates in a muscular bulb that presumably facilitates sperm transfer. 0, absent; 1, present.
41. **Prostate lobe:** Both *P. falklandica* and *P. orca* have a simple prostate with a secondary lobe. 0, absent; 1, present.
42. **Prostate texture:** In *P. finmarchica* and in *P. gibba*, the prostate is nodulose. All of the other species in our sample have smooth prostates. 0, smooth; 1, nodulose.
43. **Secondary bursa copulatrix:** Members of the *P. aperta* clade have a small bursa copulatrix

posterior to the primary bursa copulatrix at the terminus of the female reproductive system. *Philine fenestra* has two appressed secondary bursa copulatrices. 0, zero; 1, one; 2, two.

44. **Gonopore:** The gonopore in all *Philine* species is located at the posterior. The character was used to separate the in-group from the out-group because the gonopore both in *Scaphander* and in *Cylichna* is located on the right. 0, right; 1, posterior.

Nervous System

45. **Supraintestinal ganglion:** In the outgroup taxa, the supraintestinal ganglion has a posterior location. As the nervous system becomes more concentrated (cephalized), the ganglion migrates anteriorly. In some species, the supraintestinal ganglion can be anterior or adjacent to the parietal ganglion, and, in other species, it is located half-way between the visceral and parietal ganglia. 0, posterior; 1, fused to pleural; 2, adjacent to or adjoining the fused pleural-parietal ganglion.
46. **Subintestinal ganglion:** In some taxa, the subintestinal ganglion is distinct from the visceral one. In the vast majority of species, the subintestinal ganglion is adjacent to the visceral one. 0, distinct; 1, fused to visceral ganglion.

Phylogeny of the Philinidae

In the resulting phylogeny (Figure 38), 54 most parsimonious trees were retrieved after 1000 repetitions of a heuristic search using random start trees with stepwise addition. The trees had a length of 133 steps, a consistency index of 0.481, and a retention index of 0.693. Whether *Scaphander* or *Cylichna* was used as a single outgroup or both were used together, a monophyletic Philinidae was obtained and the tree topology was identical. In the phylogeny, *P. falklandica* is the most basal taxon and is the sister to the rest of *Philine*. Immediately above this node is a trichotomy with *P. gibba*, the clade containing *P. alba* and *P. alboides* and a clade containing the remainder of *Philine*. Within this remainder of *Philine* is a clade containing *P. berghi* and *Spiniphiline kensleyi* and two other larger clades. The smaller of these clades contains *P. orca*, *P. quadrata*, *P. lima*, and *P. pruinosa*. The sister clade to this smaller clade is the large *P. aperta* clade containing 15 species. At and near the base of the *P. aperta* clade are two small clades with *P. finmarchica* and *P. thurmami* as sister species followed by *P. infundibulum* and *P. sarcophaga* as sister species. These are followed by a grade of three species, *P. babai*, *P. fenestra*, and *P. auriformis*. The majority of species in the *P. aperta* clade are in the large clade of species that are characterized by having gizzard plates with paired

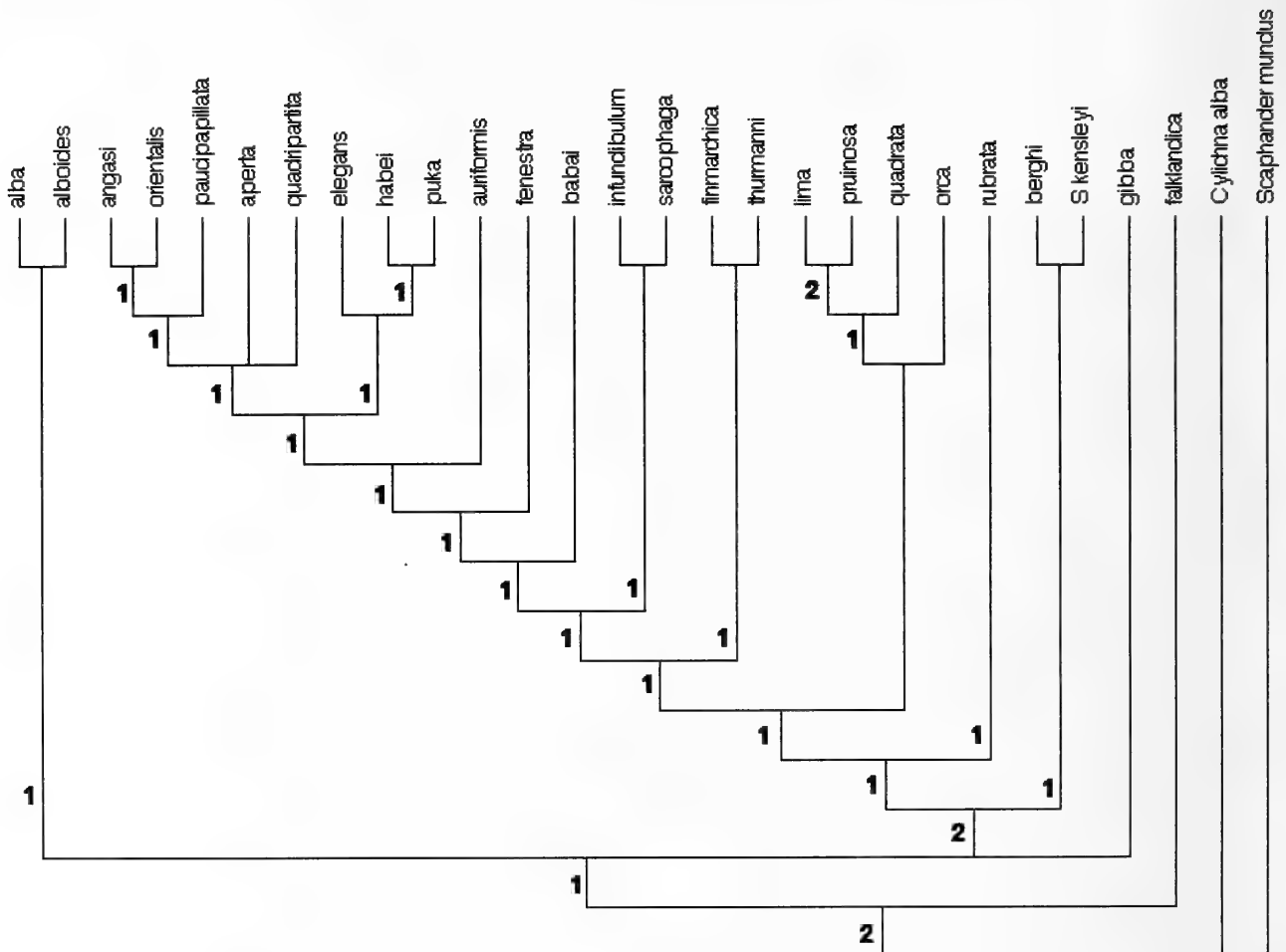


Figure 38. Strict consensus tree of *Philine* phylogeny showing Bremer support.

pores. These clades consist of two clades, the one that contains *P. elegans*, *P. habei*, and *P. puka* and a larger clade composed of *P. quadripartita*, *P. aperta*, *P. paucipapillata*, *P. orientalis*, and *P. angasi*.

A decay analysis of the resulting strict consensus (Figure 38) shows only moderate support for the resulting clades. Only three clades have a Bremer support value of 2, whereas each remaining clade has a value of 1. The clades with a support value of 2 are the clade of all *Philine*, the clade containing all members of *Philine* except *P. falklandica*, *P. gibba*, *P. alba*, and *P. alboides* (henceforth referred to as the derived-*Philine* clade), and the clade of *P. lima* and *P. pruinosa*. This fact strongly suggests that additional studies should be undertaken to investigate the phylogenetic relationships of *Philine*. Despite the low Bremer support, several nodes are supported by multiple characters (Figure 39). *Philine* is supported by four characters. The derived *Philine* clade is supported by eight synapomorphies. The *P. aperta* clade is supported by five synapomorphies. The clade containing the species with paired pores of the

gizzard plates (the pored-*Philine* clade) is also supported by five synapomorphies.

Character Evolution

Several external morphological characters are oddly distributed in the resulting tree. For example, the relative length of the cephalic and posterior shields (character 2) is extremely variable, as is the presence or absence of a posterior notch (character 4). It is likely that these represent preservational artifacts rather than being representative of characters that exhibit little phylogenetic signal. It is imperative that external morphological characters be observed in living specimens whenever possible.

The resulting tree indicates that pigmented rather than white body color (character 1) evolved more than once in two distinct lineages. Again, additional documentation of color pattern in living specimens is necessary to obtain a better understanding of the evolution of pigmentation in *Philine*.

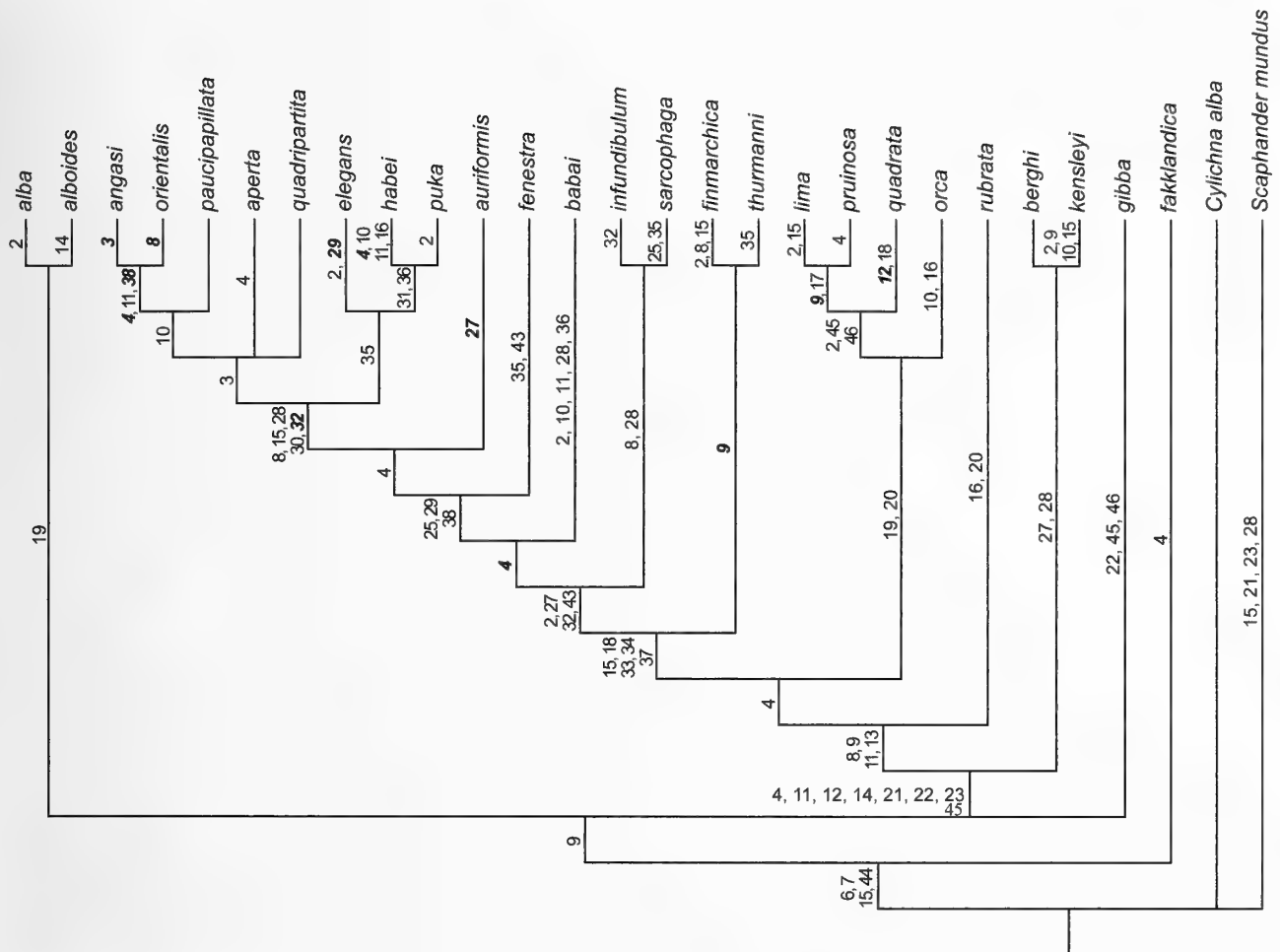


Figure 39. Strict consensus tree of *Philine* phylogeny showing character distribution. Characters in italics represent reversals.

The presence of thick parapodial lobes (character 3) is found only in the large shallow-water species of the pored-*Philine* clade (*P. orientalis*, *P. paucipapillata*, *P. aperta*, and *P. quadripartita*), but it seems to be absent in *P. angasi*.

It seems that most basal members of *Philine* have smooth shells without punctate sculpture (character 8). However, Gosliner (1994) argued that presence of punctate shell sculpture is plesiomorphic in opisthobranchs. Punctate sculpture is present in many of the moderately derived species of *Philine*. Although this might represent a reversal in these taxa, a more plausible scenario is that sculpture is not entirely lost in any *Philine* species but is present in postmetamorphic individuals. This scenario is supported by the fact that some postveliger shell regions of some specimens of *P. orientalis* have punctate sculpture, whereas other adult specimens entirely lack any evidence of such sculpture. It appears that subsequent shell calcification covered the layers that had bare sculpture. Well-developed sculpture seems to be present in adults of some species

that attain a relatively small body size, further suggesting that sculpture may be ontogenetically linked to shells that are immediately postmetamorphic or in species that mature at a smaller body size and are probably pedomorphic. The same developmentally linked aspects also may be related with the apparent reversal of shell coiling patterns (character 9), which may be linked to pedomorphosis.

Characters 10 and 11, relating to the number of dorsal and ventral oral glands, indicate that derived conditions might have evolved independently or may represent a preservational artifact. These glands are often difficult to find in poorly preserved animals.

The presence of elongate salivary glands (character 12) characterizes the outgroup taxa and basal members of *Philine*. Elongate salivary glands are also present in the more derived *P. quadrata*.

A large radula relative to the size of the body (character 13) is characteristic of the outgroup and more basal *Philine* species. In more derived taxa, the size of the radula becomes reduced. Other radular

features, such as loss of the rachidian tooth (character 14) and reduction in the number of lateral radular teeth (character 15) are found in more highly derived members of *Philine*. Presence of two outer laterals per side is characteristic of the *P. aperta* clade, with a further reduction to a single outer lateral per side in the pored-*Philine* clade.

The presence of a distinct crop (character 18) is found in the more basal members of *Philine*. Presence of an indistinct crop is another important synapomorphy of the *P. aperta* clade and is also found in *P. quadrata*.

The presence of spindle-shaped gizzard plates (character 21), as well as the presence of large plates (character 23), unites all taxa in the derived-*Philine* clade, as does the presence of an esophagus with a distinct tube (character 22). Other characters of gizzard-plate shape provide additional significant synapomorphies that unite larger clades. The clade that includes the subclade of *P. sarcophaga* and *P. infundibulum* and its sister group all have paired gizzard plates and one plate that is of a different size (character 27). This condition seems to have been reversed in *P. auriformis*, where all three plates are equal in size. In the pored-*Philine* clade, all taxa have an unpaired plate (character 28) that is smaller than the paired plates. This condition also unites *P. berghi* and *S. kensleyi*. In *P. sarcophaga* and *P. infundibulum*, the unpaired plate is larger than the paired ones. The presence of pores (character 30) unites the pored-*Philine* clade.

Several features of the reproductive system also provide important synapomorphies. Presence of an elongate, convoluted prostate gland (character 33), a hammer-shaped penial papilla (character 34), and presence of a separate ejaculatory duct (character 37) unite the *P. aperta* clade. The presence of a secondary bursa copulatrix (character 43) is synapomorphic for the clade that includes the subclade of *P. sarcophaga* and *P. infundibulum* and its sister group. Presence of a posteriorly situated gonopore (character 44) is synapomorphic for *Philine*.

It is evident that characteristics of radular morphology, the elaboration of the gizzard plates, the form of the penial complex, and the presence of exogenous sperm storage organs provide most of the characters that provide the structure of the tree presented. Most external morphological characters and characteristics of the nervous system appear to be less significant in shaping the phylogeny of *Philine*.

DISCUSSION

The majority of the species of *Philine* have been described strictly from the shell (see Pilsbry, 1895, for an example). There seems to be a great deal of convergence in shell morphology, and, as we reveal with our analysis of the *P. aperta* species complex,

species with similar shells can have dramatically different anatomical features. Although conchological features may provide useful taxonomic characters in other clades—and perhaps even in other genera of Philinidae—more recent studies (Marcus & Marcus, 1966, 1969; Rudman, 1970, 1972b; Marcus, 1974; Gosliner, 1988) have demonstrated the necessity of describing detailed anatomical features to provide for definitive identification of species. Despite this fact, new species continue to be described from shells only (e.g., Linden, 1995). This creates great uncertainty as to the identity of species, and it makes it particularly difficult to reconcile conchological features with anatomical ones to produce an integrative taxonomy. Although the shell is important in identifying members of the genus *Philine* as it currently stands, it is not sufficient for determining the number of species within the groups, for deciphering relationships among the species, or for the identification of supraspecific taxa.

Our results indicate that the *P. aperta* species complex is a clade. Earlier systematists have synonymized many of the species in this clade, agreeing that all or most of the species that possess pores on their plates represent a single species or very few species. For example, in distinguishing between *P. aperta* and *P. orientalis*, Lemche (1948) cited Bergh (1901) as saying that “the number of species already established on [this] variation ... is sufficiently large.” What makes this quotation most amusing, perhaps, is that Lemche thought Bergh was synonymizing *P. aperta* and *P. quadripartita* rather than *P. aperta* and *P. orientalis*. This oversynonymization is surprising in that these taxa inhabit disparate biogeographical regions where the rest of the biota does not overlap. By including a breadth of anatomical characters, including (but not limited to) gizzard plates and shell morphology, we have been able consistently to distinguish species within the *aperta* clade. Our cladistic analysis does not fully resolve the phylogeny of the clade, but it does demonstrate monophyly. Thus, the phylogenetic results combined with our anatomical descriptions clearly indicate that several species comprise the *aperta* clade.

Other large clades are clearly monophyletic, although Bremer support values are low. The fact that morphological characters alone do not provide a robust phylogeny strongly suggests that additional phylogenetic studies of *Philine* should include molecular phylogenetic data.

The form of the shell has traditionally been used to subdivide the genus *Philine* into different genera. For example, Laona A. Adams, 1865, for *Laona zonata*, A. Adams, 1865, was known only from a shell. Later, Pruvot-Fol (1954) included species in this genus that lacked gizzard plates. Later authors (Rudman, 1972b; Marcus, 1974; Gosliner, 1980, 1988) concluded that these genera are artificial and unnecessary. The present

study sheds additional light on these issues. The species included in *Laona*, which lack gizzard plates, form a clade in the present analysis. However, recognition of *Laona* as a distinct taxon renders *Philine* paraphyletic. The same is true for *Spiniphiline* Gosliner 1988. *Spiniphiline* was erected to accommodate a species with several autapomorphic features, most notably spines on the shell. Nevertheless, *Spiniphiline* is nested within *Philine*, and its separation again makes *Philine* paraphyletic. Maintenance of these taxa serves no useful purpose, and these taxa should be regarded as synonyms of *Philine*, especially in light of the fact that the majority of Philinidae are still known only from shells and that our phylogeny has little Bremer support. Subsequent revision of classification and nomenclature is necessary at some point, but it is premature to consider genera other than *Philine*, given the amount of missing data for the majority of its constituent species.

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Age and Growth of *Glossocardia obesa*, a “Large” Bivalve in a Submarine Cave Within a Coral Reef, as Revealed by Oxygen Isotope Analysis

AKIHISA KITAMURA

Institute of Geosciences, Faculty of Science, Shizuoka University, Shizuoka 422-8529, Japan
(e-mail: seakita@ipc.shizuoka.ac.jp)

KEIGO TADA

Faculty of Environmental Earth Science, Hokkaido University, N10W5 Sapporo, 060-0810, Japan

SABURO SAKAI

Institute for Research on Earth Evolution, Japan Agency for Marine-Earth Science and Technology, Yokosuka 237-0061, Japan

NAGISA YAMAMOTO, TAKAO UBUKATA

Institute of Geosciences, Faculty of Science, Shizuoka University, Shizuoka 422-8529, Japan

TSUZUMI MIYAJI

Department of Earth and Planetary Science, University of Tokyo, Tokyo 113-0033, Japan

AND

TOMOKI KASE

National Science Museum, Tokyo, 169-0073, Japan

Abstract. Dark submarine caves are unique habitats from which most coastal species are excluded because of darkness, marked oligotrophy, and reduced water circulation. Many bivalves have been found in caves of tropical West Pacific coral reefs, but nearly all reported species are very small in adult shell size, generally <5 mm in length. *Glossocardia obesa* (Reeve, 1843) is an exceptionally large bivalve in the cave fauna and grows to 80 mm in adult shell length. Since live specimens of *G. obesa* are apparently very uncommon, there has been no study on its life-history traits. We performed an oxygen isotope analysis of a *G. obesa* (72 mm in shell length) collected alive in a submarine cave at Okinawa Islands, Japan. The $\delta^{18}\text{O}$ record is divided into early- and late-growth phases. There is no systematic change in $\delta^{18}\text{O}$ value in the early-growth phase, whereas the $\delta^{18}\text{O}$ record for the late-growth phase contains six cycles. Comparing the $\delta^{18}\text{O}$ -derived temperatures from *G. obesa* with water-temperature records and $\delta^{18}\text{O}$ value of seawater in the cave shows that the $\delta^{18}\text{O}$ cycles of *G. obesa* reflect seasonal variation in water temperature. This result demonstrates that the oxygen isotope analysis can usefully be employed to estimate growth and age in this species.

INTRODUCTION

Sheltered, submarine caves developed within coral reefs are inhabited by unique invertebrate communities that include “living fossil” species and relatives of deep-sea taxa (Jackson et al., 1971; Jackson & Winston, 1982; Vermeij, 1987; Harmelin, 1997). Many workers have addressed the ecological and evolutionary significance of the cryptic communities (Reitner & Gautret, 1996;

Kano et al., 2002; Motchurova-Dekova et al., 2002; Kano & Kase, 2008; Ubukata et al., 2009). Kase & Hayami (1992) and Hayami & Kase (1993, 1996) investigated cavernicolous bivalves from many caves in Ryukyu Islands, Bonin Islands, Philippine Islands, Saipan, Palau, and Guam, and reported >60 species, many of which share the following characteristics: (1) very small adult size (usually <5 mm in length); (2) unusually large prodissoconch I and an absence of

prodissococonch II in many species, implying nonplanktotrophic development; and (3) persistent denticles on the provinculum retained until the adult stage in many pteriomorph species, suggesting significant paedomorphosis by progenesis. Kase & Hayami (1992) interpreted these characteristics to indicate a relatively small number of larvae and a predominantly K-selected reproductive strategy. The authors regarded these ecological features as adaptations to nutritional deficiency in the submarine caves, as widely documented by Fichez (1990, 1991).

Although most of the bivalves in the caves are very small in adult shell size, the trapeziid *Glossocardia obesa*, a shallow infaunal suspension feeder, is an exceptionally large bivalve in the cave fauna (Hayami & Kase, 1993). Shell length exceeds 80 mm and the shell volume is over $\times 2000$ greater than those of other cavernicolous microbivalves. Hayami & Kase (1992, 1996) reported that the soft part of *G. obesa* is much smaller than that expected for their shell size; however, their soft bodies are still much larger than those of other cavernicolous microbivalves.

This species, distributed in the tropical West Pacific region, lives in both the open sea and cryptic environments such as submarine caves developed within coral reefs (Matsukuma & Habe, 1995). Morton (1979) described this bivalve as a deepwater species, and it has also been recorded in shelly gravel bottoms at between 5- and 60-m water depth (Okutani, 2000). However, there has been no study of the life-history traits of *G. obesa* because it is very rare to encounter living individuals in either the open sea or cryptic environments such as submarine caves.

In this paper, we examined the pattern and rate of shell growth of a single specimen of *G. obesa* collected alive in a submarine cave developed within a coral reef (Figure 1), from the perspective of oxygen isotope profiles. This method is commonly used to decipher the life-history traits of living and extinct bivalve species (e.g., Jones et al., 1983, 1986; Tanabe & Oba, 1988; Goodwin et al., 2001; Schöne et al., 2003; Watanabe et al., 2004). The proportion of different isotopes of oxygen present in the shell carbonate reflects the ambient water temperature in which the shell was deposited because in colder water more of the heavier ^{18}O isotope is precipitated into the shell, while at higher temperatures relatively more of the lighter ^{16}O isotope is precipitated.

SHELL DESCRIPTION AND STUDY AREA

We obtained a shell of *G. obesa* collected alive by a scuba diver in the submarine Daidokutsu cave located in the northeastern coast of Ie Island, Okinawa Island (Figure 1), in early August 2004. The cave's entrance lies about 19 m below sea level. The cave is 40 m long,

dark inside, and deepens inward to its deepest point at 29 m below sea level. The floor is covered by >1.4 m of calcareous mud (Kitamura et al., 2007a). So-called living fossils, including the gastropod *Neritopsis radula* and the bivalve *Pycnodonte taniguchii*, have been found alive in the cave (Hayami & Kase, 1992; Kase & Hayami, 1992). In addition, at least 36 species of cavernicolous microbivalves have been identified from the sediments of the cave (Kitamura et al., 2007a). Kitamura et al. (2007b) measured water temperatures hourly in the cave from July 26, 2003 to July 6, 2004, documenting seasonal variation from 21°C (February) to 29°C (late August to early September; Figure 2A).

METHODS

Water samples for oxygen isotope analyses were collected within Daidokutsu and upon the reef slope at 30-m depth on July 2, 2007 (10:50–11:15 a.m. Japan time; Figure 1). Oxygen isotope analyses of the water ($\delta^{18}\text{O}_w$) were undertaken at the Geo-Science Laboratory in Nagoya, Japan, using a Finnigan MAT delta S. $\delta^{18}\text{O}_w$ ratios are reported relative to Vienna Standard Mean Ocean Water (V-SMOW), and the analytical precision (1 SD) was better than $\pm 0.1\text{‰}$. Salinity and temperature were measured using a temperature–salinity meter at the time of collecting water samples.

The specimen of *G. obesa* was embedded directly in polyester resin without any chemical treatment, and cut along the axis of maximum growth. The section was ground with 1200 *sic* grit, polished with 3- μm Al_2O_3 powder, and photographed under transmitted light. Powdered carbonate samples were collected from the outer shell layer using an automated Micromill sampler at the Japan Agency for Marine–Earth Science and Technology (JAMSTEC), Japan (Sakai, 2007). The width of the sample grooves was 2 mm (80–120 mg in weight) from the umbo down to 52 mm, and the width was 1 mm (50–70 mg in weight) from the 52-mm point to the shell margin. The powdered carbonate samples received no additional thermal or chemical treatment prior to oxygen isotope analysis. The sample was analyzed using a mass spectrometer (IsoPrime, Micro-mass) at JAMSTEC. Individual samples were reacted with 100% phosphoric acid at 90°C. Oxygen isotope values of shell carbonate ($\delta^{18}\text{O}_c$) are reported relative to Pee Dee belemnite, and the analytical precision (1 SD) was better than $\pm 0.1\text{‰}$. X-ray diffractometer analysis revealed that the shell of *G. obesa* consists entirely of aragonite.

RESULTS

There is no significant difference in both salinity and $\delta^{18}\text{O}_w$ between inside the cave and at 29-m depth (Table 1). The $\delta^{18}\text{O}_w$ –salinity relation is similar to the linear relationship proposed by Oba (1988) for surface

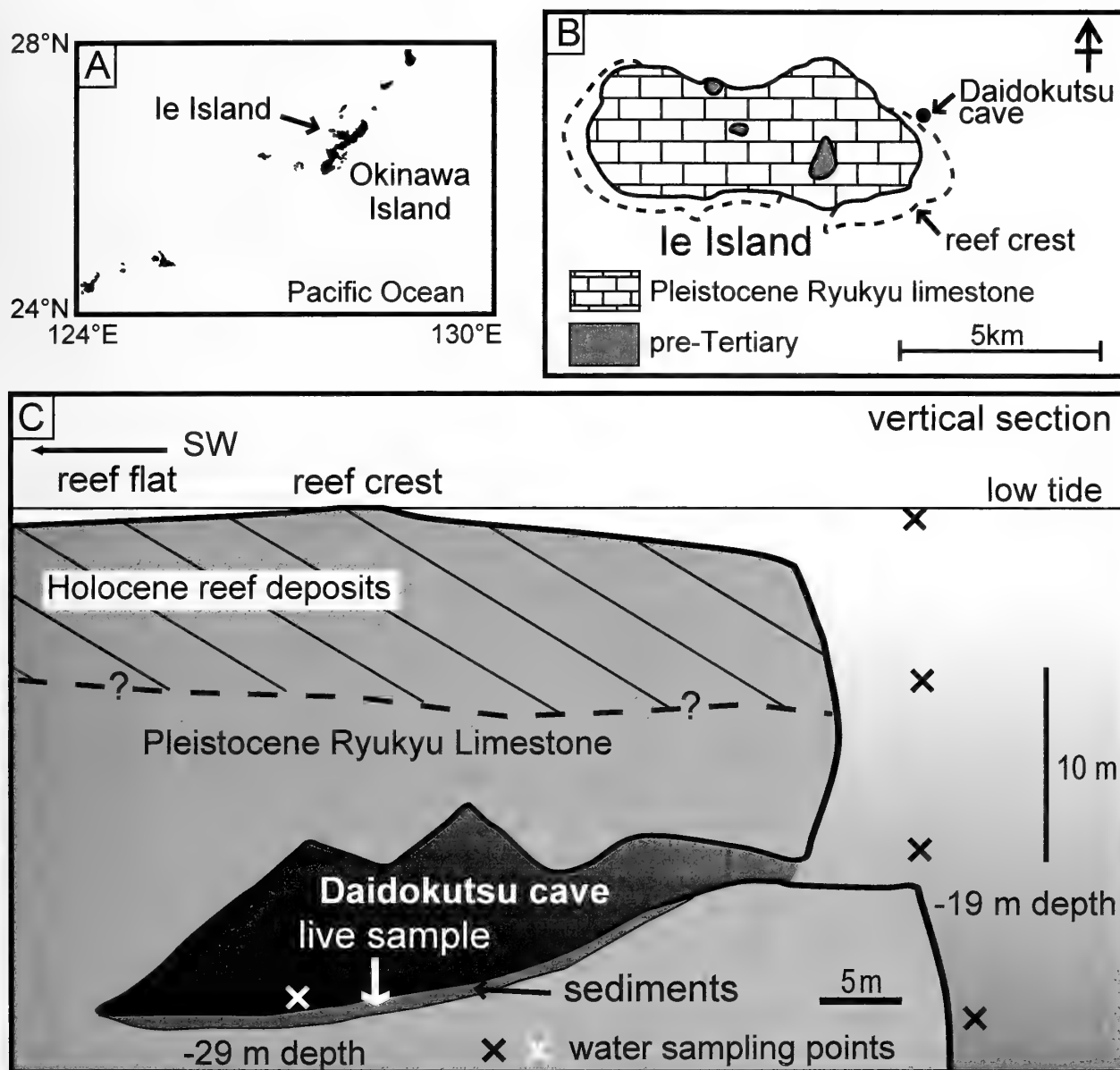


Figure 1. Locality map showing sampling site for *Glossocardia obesa* and Daidokutsu cave.

water extending from the East China Sea to the Kuroshio Current off the southern Japanese Islands, which is $\delta^{18}\text{O}_w = 0.203 S - 6.76$ (S = salinity).

Seven translucent growth lines with widths of 0.9–1.3 mm were observed in the outer shell layer under transmitted light (Figure 3). The $\delta^{18}\text{O}_c$ record is divided into early- and late-growth stages at a point located about 34 mm from the umbo (Figure 3). The early-growth stage shows no systematic variation in $\delta^{18}\text{O}_c$ values, which range from -1.8 to 0‰ . In contrast, the $\delta^{18}\text{O}_c$ record for the late-growth stage contains six cycles (Cycles 1 to 6; Figure 3) for which the wavelength decreases with distance from the umbo.

These six cycles are subdivided into four earlier cycles (1–4) and two later cycles (5 and 6). The $\delta^{18}\text{O}_c$ values in the former range from -2.6 to -0.8‰ , while in the latter from -2.0 to -1.2‰ . There are two translucent growth lines in Cycle 1, but only a single growth line was observed in each of the later cycles. These lines correspond to light oxygen isotope values in each cycle (Figure 3). There are anomalously high $\delta^{18}\text{O}_c$ values at a point located 26 mm from the umbo and at the shell margin. Such exceptionally heavy $\delta^{18}\text{O}_c$ values were often reported from other bivalves, such as *Mesodesma donacium* (Carré et al., 2005), but their origin remains poorly understood.

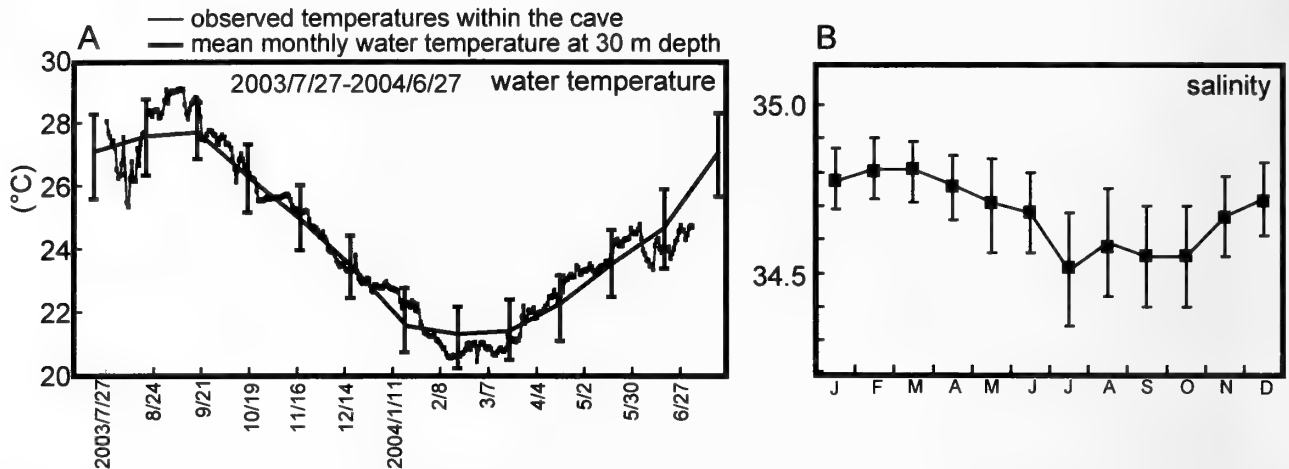


Figure 2. **A**, Comparison of observed temperatures with mean monthly water temperature at 29-m depth (the JODC). Data of observed temperatures within the cave are from Kitamura et al. (2007b); **B**, Seasonal variations in salinity at 29-m depth. Data are sourced from database compiled by the JODC. Error bars of monthly temperature and salinity represent standard deviation (1σ) from monthly value for the period between 1906 and 2003.

DISCUSSION

It is generally accepted that the oxygen isotopic composition of bivalves is influenced by the temperature and isotopic composition of the ambient seawater in which the animal formed its shell. As noted above, $\delta^{18}\text{O}_w$ in the cave is equal to that at 29-m water depth. In addition, the relationship between $\delta^{18}\text{O}_w$ and salinity inside and outside the cave is not considerably different than that previously proposed by Oba (1988). Therefore, seasonal variation in $\delta^{18}\text{O}_w$ within the cave can be estimated using salinity data at 30-m depth (S_{30m}), as compiled by the Japan Oceanographic Data Center (JODC; $1 \times 1^\circ$ grid cells, latitude $26\text{--}27^\circ\text{N}$ and longitude $127\text{--}128^\circ\text{E}$, data from the period 1874–2001), and the above $\delta^{18}\text{O}_w$ –salinity relationship (Oba, 1988).

Based on the data of JODC, S_{30m} ranges from 34.5 in summer to 34.8 in winter (Figure 2B). We regarded the $\delta^{18}\text{O}_w$ value in the cave for the entire year to be $0.3 \pm 0.03\text{‰}$ if the $\delta^{18}\text{O}_w$ –salinity relationship is adopted.

Table 1

Oxygen isotope values obtained for water sampled from within Daidokutsu cave and upon the reef slope off Ie Island, Okinawa, Japan. Locations of sampling points are shown in Figure 1.

Area	Reef slope				Daidokutsu
Depth (m)	0	10	20	30	29
Temperature ($^\circ\text{C}$)	29.2	28.0	27.5	26.6	25.2
Salinity	33.4	33.1	33.2	34.2	34.3
$\delta^{18}\text{O}_w$ (‰; vs. V-SMOW)				0.4	0.3

Water temperatures were calculated using the equation of Carré et al. (2005):

$$T(^{\circ}\text{C}) = (17.41 \pm 1.15) - (3.66 \pm 0.16)(\delta^{18}\text{O}_{\text{argonite}} - \delta^{18}\text{O}_w).$$

Except for two exceptionally heavy $\delta^{18}\text{O}$ values, all $\delta^{18}\text{O}_c$ -derived temperatures based upon using the equation of Carré et al. (2005) fell within the temperature range in the cave (Figure 4). The 6.5°C variation in $\delta^{18}\text{O}$ -derived temperature is ca. 81% of the annual range of temperatures in the cave from July 26, 2003 to July 6, 2004 (8°C). We therefore consider that the $\delta^{18}\text{O}_c$ cycles reflect seasonal fluctuations in water temperature. The relatively small amplitudes of Cycles 5 and 6 may reflect a decrease in sampling resolution due to a slowdown or cessation in shell growth. The relationship between translucent growth lines and $\delta^{18}\text{O}_c$ profiles indicates that these lines were formed during warm seasons (Figures 3, 4). This interpretation is consistent with the fact that the shell margin (i.e., the most recently formed shell material) of the study specimen collected in early August 2004 is not translucent. If this relationship is assumed, the last translucent growth line (Cycle 6) is supposed to have been formed during the warm season of 2003. This result demonstrates that oxygen isotope analysis appears to work well for this species and has the potential to provide useful growth and age estimates.

We analyzed the pattern of the growth curve of shell length against annual growth lines (translucent growth lines) in the specimen based on the number of seasonal cycles of $\delta^{18}\text{O}_c$ (Figure 5). A series of measured data was approximated by the von Bertalanffy equation and a best-fit curve to the data was numerically calculated

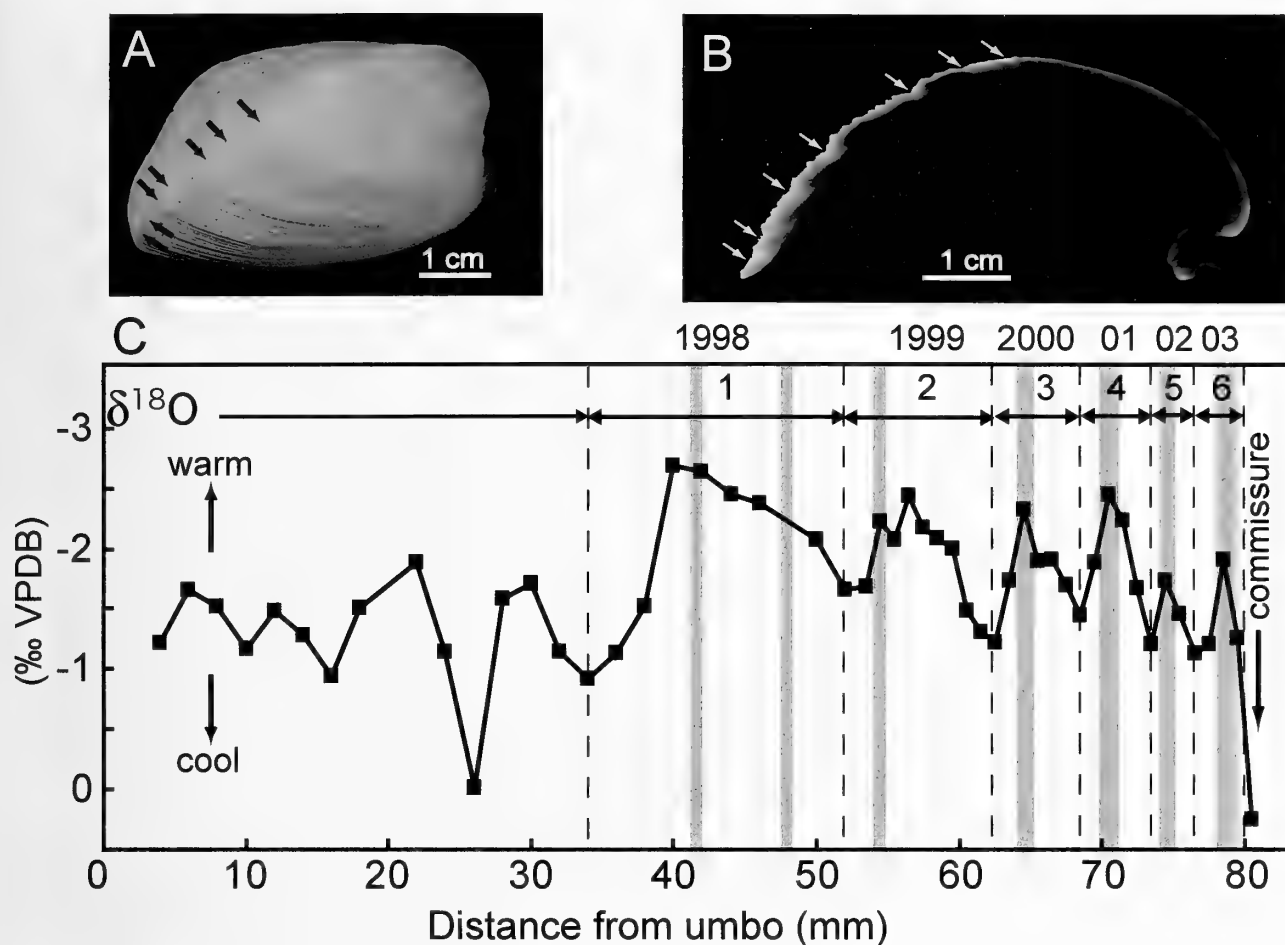


Figure 3. **A**, Exterior of left valve; **B**, Optical transmitted-light photograph of the longitudinal shell section. Arrows show translucent growth lines; **C**, Oxygen isotopic profile for our specimen of *Glossocardia obesa*. Vertical gray bars represent the location of translucent growth lines. Numbers 1–6 are inferred to be cycles bounded by neighboring troughs.

with a least-squares method. Because a seasonal cycle of $\delta^{18}\text{O}_c$ was unclear in the early-growth stage, we assumed the following two cases for regression analyses: (1) the bivalve regularly formed each annual growth line in every summer through which the shell has passed (Case I), and (2) the animal failed to form one or a few distinct annual lines in the early-growth stage (Case II). In Case I, the first translucent growth line is supposed to have been formed within 1 yr after hatching. In this case, the beak point with shell length of 0 mm was regarded as the “zeroth” annual increment and the plot of (0,0) was used together with biometric data for regression analysis. On the other hand, if we assume Case II, it took longer than 1 yr until the first annual growth line was formed and the “zeroth” annual increment does not represent the start of the shell growth. In the latter case, therefore, the plot of (0,0) was not used for regression analysis. The fitness of observed data to the von Bertalanffy curve supports

Case II rather than that of Case I (Figure 5). The result suggests that the bivalve started to form annual lines in the second summer or later and lived for at least 8 yr until 2003 (Figure 4).

Combining oxygen isotope analysis with an analysis of absolute growth pattern allow us a reasonable estimation of age and life-history traits of *G. obesa*. Studies on the life-history strategy of this species may provide a clue to reveal the reason why such a “huge” bivalve is a constituent of the refugial community dominated by microshells.

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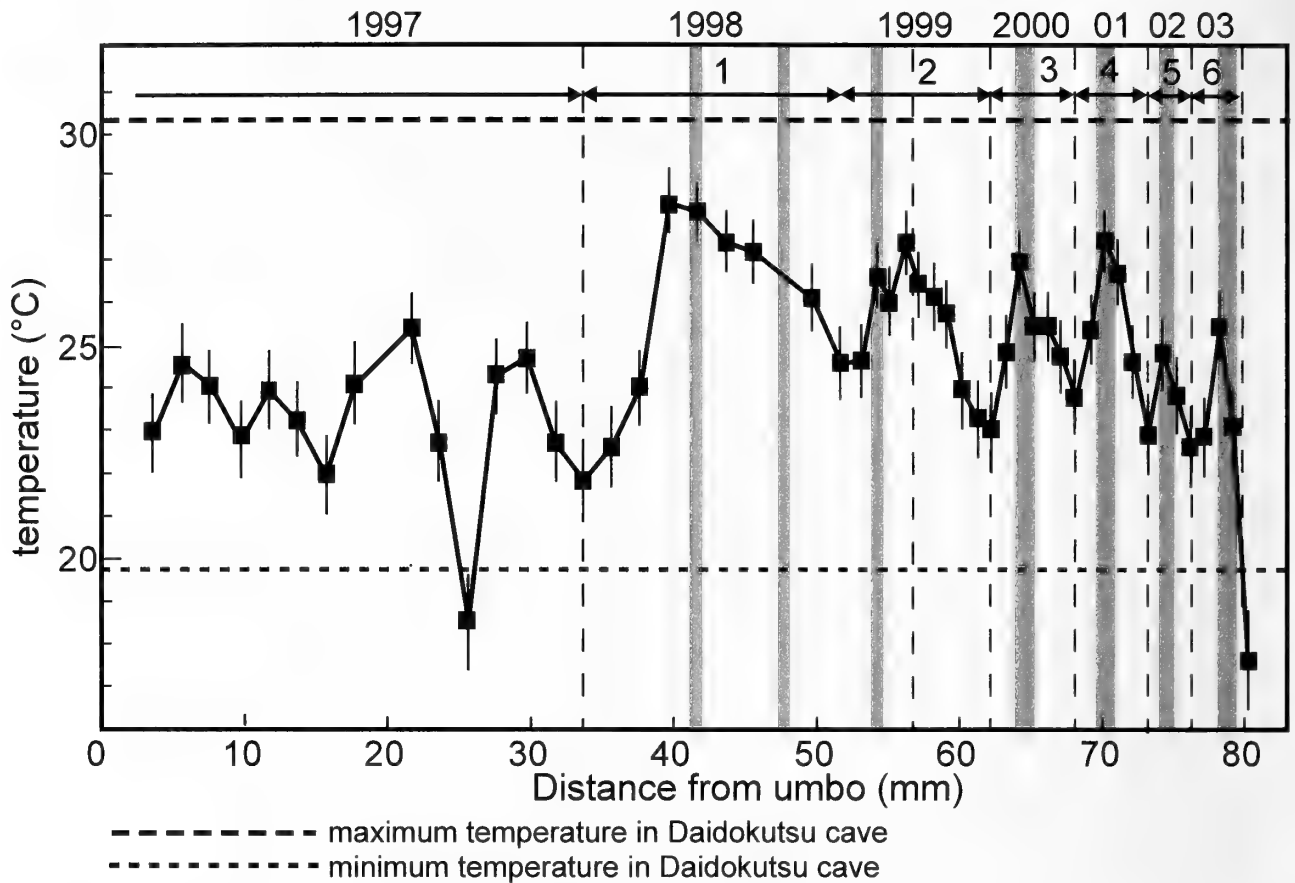


Figure 4. Reconstructed temperature record based on shell oxygen isotope data using the equation of Carré et al. (2005).

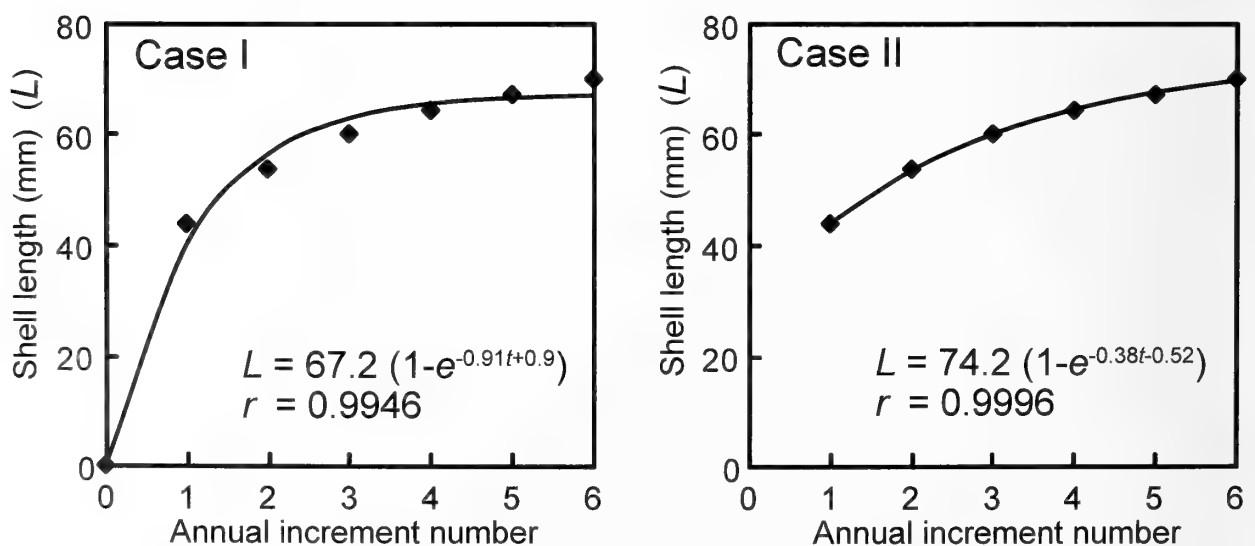


Figure 5. Predicted von Bertalanffy growth curves estimated in the two cases: I, the first annual growth line was formed in the first summer; or II, it was recorded in the second summer or later.

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Field Experiments on the Feeding of the Nudibranch *Gymnodoris* spp. (Nudibranchia: Doridina: Gymnodorididae) in Japan

RIE NAKANO AND EUICHI HIROSE

Department of Chemistry, Biology, and Marine Science, Faculty of Science, University of the Ryukyus, Nishihara,
Okinawa 903-0213, Japan

Abstract. We report field experiments of the diets of certain *Gymnodoris* species (Nudibranchia: Doridina: Gymnodorididae) that inhabit the seas in the vicinity of Japan. Of 21 individuals of five predatory species, 13 fed on 14 of the 44 prey individuals. Among these predators, five individuals of four species located the mucus trail of their prey and pursued it. After touching the prey with their oral tentacles, most predators everted the buccal apparatus to capture the prey. Two modes of feeding occurred: biting off part of the prey or swallowing it whole. Some predator and prey combinations have not previously been reported, to our knowledge: *Gymnodoris alba* fed on *Vayssiorea felis* (Nudibranchia: Doridina: Vayssioreidae), and *G. okinawae* fed on *Metaruncina setoensis* (Cephalaspidea: Runcinidae). We also found an unknown gymnodorid that fed on several *Elysia* spp. and *Thuridilla vatae*. The unknown predator was similar in morphology to *G. alba*, but its prey items were similar to those of *G. okinawae*.

INTRODUCTION

The opisthobranchs (Gastropoda: Mollusca) demonstrate various food habits: Sacoglossa, Anaspidea, and some species of Cephalaspidea are herbivorous, and others are carnivorous (see Behrens, 2005). Carnivorous opisthobranchs feed on specific prey items, including sponges, hydroids, bryozoans, entoprocts, and ascidians; for example, each sponge-feeding species feeds only on specific sponge species (Rudman & Bergquist, 2007).

Many carnivorous species feed on opisthobranchs, as well as on nonopisthobranchs. For example, Cattaneo-Vietti et al. (1993) reported that *Pleurobranchaea maculata* (Quoy & Gaimard, 1832) (Notaspidea: Pleurobranchidae) fed on polychaete worms, amphipods, ophiuroids, dead squids, and dead fishes, as well as opisthobranchs, e.g., *Philine argentata* Gould, 1859 (Cephalaspidea: Philinidae), *Ringicula doliaris* Gould, 1860 (Cephalaspidea: Ringiculidae), and their conspecifics. Among the opisthobranchs that are known to feed on other opisthobranchs are *Chelidonura* spp., *Navanax inermis* (Cooper, 1863), *Philineopsis* spp., *Pleurobranchaea maculata* (Quoy & Gaimard, 1832), *Gymnodoris* spp., *Roboastra leonis* Pola, Cervera & Gosliner 2005, *Melibe* spp., and *Godiva* sp. (Paine, 1963; Kay & Young, 1969; Rudman, 1972; Farmer, 1978; Kay, 1979; Gosliner, 1987; Cattaneo-Vietti et al., 1993; Gosliner et al., 1996; Battle & Nybakken, 1998).

Gymnodorids (Nudibranchia: Doridina: Gymnodorididae) usually feed on opisthobranchs and/or their eggs, but not on other organisms. *Gymnodoris nigricolor* Baba, 1960 is one exception that apparently captures

certain goby species (Osumi & Yamasu, 1994), such as *Amblyeleotris japonica* (Williams & Williams, 1986), by grasping their fins with the buccal apparatus. This species does not eat the entire goby, but just the fleshy tissues of the fins. The diet of each gymnodorid encompasses a particular range of species, with some feeding on various orders of nudibranchs and some having more selective diets. For instance, *G. rubropulosa* (Bergh, 1905) feeds on various genera of the family Chromodorididae, including *Hypselodoris iacula* Gosliner & Johnson, 1999, *H. festiva* Adams, 1861, *Chromodoris annae* Bergh, 1877, *C. strigata* Rudman, 1982, *Chromodoris* sp., and *Mexichromis multituberculata* (Baba, 1953) (Behrens, 2005; Nakano et al., 2007), whereas *G. aurita* (Gould, 1852) is known to feed only on *Marionia* spp. (Nudibranchia: Dendronotina: Tritoniidae) (Behrens, 2005).

The diet species of 11 gymnodorids have been reported. Table 1 summarizes the predator/prey species, including some unpublished observations (Takahashi, Natani, Hoson, Matsuda, personal communications: see Figure 1). The diets of some gymnodorids in Table 1 are laboratory diets (Young, 1969; Hughes, 1983; Johnson & Boucher, 1983) and may not represent natural food habits. The laboratory conditions may also have resulted in unusual opisthobranch behaviors. For example, Johnson & Boucher (1983) reported that *G. okinawae* Baba, 1936 did not feed on *Elysia* in aquaria, but Nakano et al. (2007) observed *G. okinawae* feeding on *Elysia* spp. in the field.

Field observations are more reliable than laboratory observations in understanding natural food habits;

Table 1
Summary of the preceding studies on the diets of *Gymnodoris* spp.

Predator	Prey	Condition	Reference
<i>G. alba</i> (Bergh, 1877)	<i>Aeolidiella</i> sp.	Undescribed	Kay & Young, 1969; Kay, 1979
	<i>Favorinus</i> sp.	Undescribed	Kay & Young, 1969; Kay, 1979
	<i>Sakuraeolis modesta</i>	Laboratory	Hughes, 1983
	<i>Flabellina alisonae</i>	Laboratory	Hughes, 1983
	<i>Phyllodesmium</i> sp.	Laboratory	Hughes, 1983
	<i>Aeolidina</i> sp.*	Field	Takasaki (personal communication)
	<i>Phidiana indica</i>	Field	Natani (personal communication)
	<i>Cratena lineata</i>	Field	Matsuda & Hoson (personal communication)
<i>G. amakusana</i> (Baba, 1996)†	<i>Elysia ornata</i>	Field	Nakano et al., 2007
<i>G. aurita</i> (Gould, 1852)	<i>Marionia</i> sp.	Field	Behrens, 2005
<i>G. bicolor</i> (Alder & Hancock, 1866; < <i>G. citrina</i> ?)‡	Members of <i>Gymnodoris</i>	Undescribed	Young, 1969
	<i>Gymnodoris okinawae</i>	Undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
	The egg masses of <i>Gymnodoris okinawae</i>	Undescribed	Young, 1969
<i>G. ceylonica</i> (Kelaart, 1858)	<i>Gymnodoris plebeia</i>	Undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
	<i>Stylocheilus longicauda</i>	Undescribed	Johnson & Boucher, 1983; Rudman, 1999a, b
	<i>Nakamigawaia</i> sp.§	Field	Nakano et al., 2007
<i>G. citrina</i> (Bergh, 1875)	<i>Gymnodoris citrina</i>	Laboratory	Young, 1969
	<i>Gymnodoris citrina</i>	Field	Johnson & Boucher, 1983; Johnson, 1992
	<i>Gymnodoris okinawae</i>	Field	Johnson, 1992; Nakano et al., 2007
	<i>Gymnodoris plebeia</i>	Field	Johnson, 1992
	Several <i>Gymnodoris</i> species	Field	Johnson & Boucher, 1983
	Unknown <i>Gymnodoris</i> spp.	Field	Johnson, 1992
	Eggs of other <i>Gymnodoris</i> species	Field	Johnson & Boucher, 1983; Johnson, 1992
	Eggs of <i>Gymnodoris ceylonica</i>	Field	Johnson, 1992
	Eggs of nudibranch	Field	Nakano et al., 2007
<i>G. inornata</i> Bergh, 1880	<i>Chromodoris orientalis</i>	Laboratory	Hughes, 1983
	<i>Doriopsilla miniata</i>	Laboratory	Hughes, 1983
	<i>Gymnodoris rubropapulosa</i>	Field	Nakano et al., 2007
	<i>Dendrodoris fumata</i>	Field	Nakano et al., 2007
	<i>Glossodoris rufomarginata</i>	Field	Natani (personal communication)
<i>G. okinawae</i> Baba, 1936	Various species of the genus <i>Elysia</i>	Undescribed	Kay & Young, 1969
	Members of Elysiidae	Undescribed	Young, 1969
	Cephalaspidean	Undescribed	Johnson & Boucher, 1983
	Did not eat <i>Elysia</i>	Laboratory	Johnson & Boucher, 1983
	<i>Thuridilla</i> sp.¶	Field	Nakano et al., 2007
<i>G. rubropapulosa</i> (Bergh, 1905)	<i>Hypselodoris iacula</i>	Field	Behrens, 2005
	<i>Chromodoris annae</i>	Field	Nakano et al., 2007
	<i>Chromodoris strigata</i>	Field	Nakano et al., 2007
	<i>Chromodoris</i> sp.#	Field	Nakano et al., 2007
	<i>Hypselodoris festiva</i>	Field	Nakano et al., 2007
	<i>Mexichromis multituberculata</i>	Field	Nakano et al., 2007
<i>G. striata</i> (Eliot, 1908)	<i>Plakobranchus ocellatus</i>	Field and laboratory	Johnson & Boucher, 1983
<i>Gymnodoris</i> sp. A**	<i>Glossodoris cincta</i>	Field	Nakano et al., 2007

* Conspecific with Nakano (2004) No. 658.

† Rudman (1999c) referred *G. amakusana* as a junior synonym of *G. striata*.

‡ *Gymnodoris bicolor* (Alder & Hancock, 1866) is regarded as a junior synonym of *G. citrina* (Bergh, 1875) by many authors (e.g., Risbec, 1953; MacNae, 1958; Baba, 1960; Young, 1967), although Young (1969) described their internal morphologies discriminate *G. bicolor* from *G. citrina*.

§ “Kurobouzu” is the Japanese common name.

|| *Gymnodoris inornata* bit off the mantle of *Glossodoris rufomarginata*.

¶ “Fujiro-midorigai” is the Japanese common name.

“Kongasuri-umiushi” is the Japanese common name.

** “Shirobonbon-umiushi” is the Japanese common name.



Figure 1. *Gymnodoris* species feeding on opisthobranchs in their natural habitats. **A**, *G. alba* (left) feeding on an unknown species of suborder Aeolidina (right); **B**, *G. alba* (right) feeding on *Cratena lineata* (left); **C**, *G. alba* (left) feeding on *Phidiana indica* (right); **D**, *G. inornata* (left) feeding on *Glossodoris rufomarginata* (right). These photographs were provided by Kenji Takasaki (**A**), Tomohiro Natani (**B** and **D**), and Sayoko Matsuda (**C**). Scale bars = 10 mm.

Figure 2. *Gymnodoris okinawae* feeding on prey (p), *Elysia* sp. **B**. **A**, The predator bit the posterior part of the parapodia of the prey; **B**, The prey escaped by cutting off the parapodia (arrow), which the predator ate. Scale bar = 5 mm.

however, the field offers only chance encounters with feeding opisthobranchs, and accumulating numerous observations is difficult. Thus, an experimental approach in the field is necessary to demonstrate the range of prey species of *Gymnodoris* spp. Our field experiments were designed to reveal the range and specificity of gymnodorid diets *in situ*: we offered several opisthobranch species to gymnodorids in the field and observed whether the predators fed on the prey candidates. We also recorded the distance at which each predator first noticed the prey.

MATERIALS AND METHODS

Animals

From 2006 to 2008, we scuba- and skin-dove to collect gymnodorids and prey candidates to examine the diets of some *Gymnodoris* species inhabiting subtropical and warm temperate waters in the vicinity of Japan. Table 2 lists the collection sites, dates, and habitats. Upon collection, we measured the body length, collection depth, and water temperature of each individual. The specimens were temporarily kept in a

Table 2
Gymnodoris spp., and their prey: field experiment.

Predator	Collection site*	Body length (mm)	Prey	Collection site	Body length (mm)	Depth (m)	Water temperature (°C)	Habitat	Distance† (mm)	Feeding behavior‡	Date
<i>G. alba</i> No. 1	A	10	<i>Vayssierea felis</i>	A	2	Intertidal	16	Rock	10	Swallowed up	April 19, 2006
			Egg of <i>Vayssierea felis</i>	A	1.5	Intertidal	16	Rock	10	Swallowed up	April 19, 2006
<i>G. citrina</i> No. 1	A	15	<i>Vayssierea felis</i>	A	2	Intertidal	16	Rock	—	Ignored	April 19, 2006
			Egg of <i>Vayssierea felis</i>	A	1.5	Intertidal	16	Rock	—	Ignored	April 19, 2006
			<i>Gymnodoris alba</i>	F	10	Intertidal	16	Rock	0	Swallowed up	April 19, 2006
<i>G. citrina</i> No. 2	F	20	<i>Thuridilla carlsoni</i>	F	20	11	29	Dead coral	—	Ignored	August 26, 2006
			<i>Chromodoris rufomaculata</i>	F	5	11	29	Dead coral	—	Ignored	August 26, 2006
			<i>Glossodoris rufomarginata</i>	F	20	7	29	Dead coral	—	Ignored	August 26, 2006
			<i>Roboastra gracilis</i>	F	10	7	29	Dead coral	—	Ignored	August 26, 2006
			<i>Chelidonura inornata</i>	E	10	8	29	Sand	—	Ignored	August 27, 2006
			<i>Elysia</i> sp. A	E	4	18	29	Dead coral	—	Ignored	August 27, 2006
			<i>Halgerda tessellata</i>	E	10	18	29	Dead coral	—	Ignored	August 27, 2006
			<i>Nembrotha milleri</i>	E	80	16	29	Dead coral	—	Ignored	August 27, 2006
			<i>Chromodoris fidelis</i>	E	10	8.5	29	Dead coral	—	Ignored	August 27, 2006
			<i>Baeolidia japonica</i>	E	5	6	29	Dead coral	—	Ignored	August 27, 2006
			<i>Gymnodoris citrina</i>	E	8	4.5	29	Dead coral	0	Swallowed up	August 27, 2006
			<i>Sagaminopteron pschedelicum</i>	E	5	4.5	29	Dead coral	—	Ignored	August 27, 2006
<i>G. citrina</i> No. 3	E	12	<i>Gymnodoris okinawae</i>	E	12	6.2	25	Dead coral	0	Swallowed up	August 28, 2006
			<i>Hexabranchius sanguineus</i>	E	4	6.5	25	Dead coral	10	Touched with oral tentacles	August 28, 2006
<i>G. citrina</i> No. 4	B	10	<i>Gastropteron</i> sp. 5	B	3	5	20	Rock, occasional coral	—	Ignored	January 21, 2007
<i>G. citrina</i> No. 5	B	20	<i>Chelidonura amoena</i>	B	20	7	20	Rock, occasional coral	—	Ignored	January 21, 2007
<i>G. citrina</i> No. 6	E	10	<i>Thuridilla carlsoni</i>	E	25	5.6	25	Dead coral	—	Ignored	May 24, 2007
			<i>Dendrodoris denisoni</i>	E	55	5	25	Dead coral	—	Ignored	May 24, 2007
			<i>Chromodoris aureopurpurea</i>	E	20	4	25	Dead coral	—	Ignored	May 24, 2007
<i>G. citrina</i> No. 7	B	12	<i>Gymnodoris okinawae</i>	B	8	2	23	Rock, occasional coral	80	Swallowed up	November 15, 2007
<i>G. okinawae</i> No. 1	E	12	<i>Gymnodoris okinawae</i>	E	10	4.5	25	Dead coral	—	Ignored	August 27, 2006
<i>G. okinawae</i> No. 2	E	10	<i>Thuridilla vatiae</i>	E	10	6.2	25	Dead coral	—	Ignored	August 28, 2006
			<i>Elysia mercieri</i>	E	4	6.8	25	Dead coral	30	Swallowed up	August 28, 2006
<i>G. okinawae</i> No. 3	B	5	<i>Elysia lobata</i>	B	5	5	20	Rock, occasional coral	0	Bit off and partly fed	January 22, 2007

Table 2
Continued.

Predator	Collection site*	Body length (mm)	Prey	Collection site	Body length (mm)	Depth (m)	Water temperature (°C)	Habitat	Distance† (mm)	Feeding behavior‡	Date
<i>G. okinawae</i> No. 4	B	NR	<i>Metaruncina setoensis</i>	B	1	2	20	Rock, occasional coral	0	Swallowed up	January 22, 2007
<i>G. okinawae</i> No. 5	C	8	<i>Elysia</i> sp. B¶	C	5	7	24	Mud	10	Swallowed up	May 11, 2007
<i>G. okinawae</i> No. 6	B	10	<i>Thuridilla carlsoni</i>	B	10	4	22	Rock, occasional coral	—	Ignored	November 13, 2007
<i>G. okinawae</i> No. 7	E	15	<i>Cyerce</i> sp. # <i>Noumea simplex</i> <i>Favorinus japonicus</i> Egg mass of nudibranch <i>Moridilla brockii</i>	E E E E E	4 7 15 — 20	4 6 4 4 5	25 25 25 25 25	Dead coral Dead coral Dead coral Dead coral Dead coral	— — — — —	Ignored Ignored Ignored Ignored Ignored	May 24, 2007 May 24, 2007 May 24, 2007 May 24, 2007 May 24, 2007
<i>G. rubropapulosa</i> No. 1	C	80	<i>Chromodoris aureopurpurea</i>	C	30	8	22	Mud	0	Bit off and partly fed	May 3, 2007
<i>G. rubropapulosa</i> No. 2	C	70	<i>Chromodoris coi</i>	C	30	8	22	Mud	0	Bit off and partly fed	May 3, 2007
<i>Gymnodoris</i> sp. B No.	E	15	<i>Thuridilla vatae</i>	E	5	6	23	Dead coral	10	Swallowed up	January 13, 2008
<i>Gymnodoris</i> sp. B No. 2	D	15	<i>Chromodoris verrieri</i>	D	3	1	22	Rock, seagrass	—	Ignored	April 3, 2008
<i>Gymnodoris</i> sp. B No. 3	D	13	<i>Elysia ornata</i>	D	8	Intertidal	22	Rock, seagrass	0	Swallowed up	April 20, 2008
<i>Gymnodoris</i> sp. B No. 4	D	10	<i>Thuridilla kathae</i>	D	20	Intertidal	23	Rock, seagrass	0	Everted the buccal apparatus	April 25, 2008
			<i>Thuridilla albopustulosa</i>	D	3	Intertidal	23	Rock, seagrass	0	Touched with oral tentacles	April 25, 2008
			<i>Thuridilla splendens</i>	D	4	Intertidal	23	Rock, seagrass	—	Ignored	April 25, 2008
			<i>Thuridilla gracilis</i>	D	15	Intertidal	23	Rock, seagrass	—	Ignored	April 25, 2008

* A, Manazuru Kanagawa (35°8'N, 139°9'E); B, Hachijo Island, Tokyo (33°6'N, 139°46'E); C, Kin Okinawa Island, Okinawa (26°26'N, 127°56'E); D, Tengan Okinawa Island, Okinawa (26°24'N, 127°50'E); E, Zamami Island, Okinawa (26°13'N, 127°17'E); F, Gahi Island, Okinawa (26°12'N, 127°17'E).

† The distance at which the predator initiated the feeding behavior. "—" indicates no response at 0 mm.

‡ Processes of feeding behavior of each *Gymnodoris* individual.

§ Conspecific with Nakano (2004) No. 41.

¶ Predator fed on prey's parapodia only. Other parts of prey—head and foot, including pericardium—ran away from predator.

Conspecific with Ono (2004) No. 101. "Tsunokuro-midorigai" is the Japanese common name.

NR = No Record.

collecting jar until the *in situ* feeding experiment, which occurred when we found prey candidates (i.e., other opisthobranchs or their eggs).

We found an unknown gymnodorid that has been recorded from the intertidal zone to about 10 m deep in the vicinity of the Okinawa Islands. The morphology of this species is similar to that of *G. alba* (Bergh, 1877) in having the genital orifice immediately posterior to the cephalic hood. However, this unknown *Gymnodoris* species is distinguished from *G. alba* by its body colors: the dorsum of this species is a translucent brown covered with small yellow spots, whereas *G. alba* has an opaque white body covered with small red spots. Moreover, this *Gymnodoris* species has a square white patch in front of the gill and a triangular white patch between the rhinophores, whereas *G. alba* never has white patches. Therefore, we regarded this species as an undescribed species, i.e., *Gymnodoris* sp. B in this report.

Feeding Experiment

The gymnodorid predator was placed 80 mm from the prey candidate (another opisthobranch), on its mucus trail, and the behavior of the predator was then recorded with a video or digital camera encased in a waterproof housing. If the predator caught the prey candidate, the mode of feeding was recorded as swallowing the prey whole, sucking its body fluid, or biting off part of its body. If the predator did not chase the prey candidate within 3 min, the mucus trail distance to the prey was shortened to 30 mm. If the predator did not follow the candidate within another 3 min, the mucus trail distance was shortened to 10 mm. Then, if the predator did not pursue the prey within 3 min, it was placed on the prey candidate. If the predator did not show any feeding behavior within 3 min, we concluded that the candidate was not a prey species of the gymnodorid.

We conducted the same experiment with nudibranch egg masses: initially, the predator was placed 80 mm from the egg mass, with the distance shortened every 3 min, to 30 mm, to 10 mm, and to 0 mm, if the predator did not move toward the eggs.

RESULTS

Prey Species of *Gymnodoris* spp.

In our feeding experiments, 21 individuals of five *Gymnodoris* species were examined against 46 individuals of 38 prey candidate species. Of the gymnodorids, 13 individuals (five species) fed on 14 prey individuals (13 species). Table 2 summarizes the results. To our knowledge, we are newly reporting two combinations of predator–prey species: *G. alba* (Bergh, 1877) No. 1 feeding on *Vayssiorea felis* (Collingwood, 1881) (Nudibranchia: Doridina: Vayssiereidae) and *G. okinawae*

No. 4 feeding on *Metaruncina setoensis* (Baba, 1954) (Cephalaspidea: Runcinidae).

Feeding Behavior Processes and Distance to Locate Prey

Gymnodorids engaged in the following feeding behaviors: first, the gymnodorid predator located the mucus trail of the prey and pursued the prey. Upon reaching the prey, the predator touched the prey with its oral tentacles, and then usually everted the buccal apparatus to capture the prey. A few predators did not do this and ignored the prey. After everting the buccal apparatus, some predators fed on the prey, but others did not. Those that fed used one of the three modes detailed in the next section. Nonfeeders retracted the buccal apparatus and freed the prey candidate. Some predators did not notice or did not follow the mucus trail of the prey candidate. Even when we set the gymnodorid directly on a prey candidate, some predators ignored it.

Among the 14 gymnodorid individuals that fed on prey, five predators (four species) located and pursued the prey before touching it. *Gymnodoris citrina* (Bergh, 1875) No. 7 located its prey, *G. okinawae*, from a distance of 80 mm. When the predator almost lost the trail of its prey, it raised its upper body and swung its head from side to side, appearing to search for the prey. After locating the mucus trail again, it followed the trail and swallowed the prey. On the other hand, *G. citrina* No. 3 did not locate *G. okinawae* until we set it directly on the prey. *Gymnodoris citrina* No. 3 fed on the prey immediately after this direct contact. From a distance of 30 mm, *G. okinawae* No. 2 located the mucus trail of *Elysia mercieri* and fed on the prey. From a distance of 10 mm, *G. alba* located and fed on *Vayssiorea felis* and its eggs. Similarly, *G. okinawae* No. 5 and *Gymnodoris* sp. B located and fed on *Elysia* sp. B and *Thuridilla vatae* (Risbec, 1928), respectively. Although *G. citrina* No. 3 located *Hexabranhus sanguineus* from a distance of 10 mm and touched it, it did not feed on it.

The other nine predators crawled randomly around the prey mucus trails until they happened to touch the prey, at which point they everted the buccal apparatus to attack, and then fed on the prey. Interestingly, although *G. citrina* No. 1 fed on *G. alba* that had just fed on *Vayssiorea felis*, *G. citrina* No. 1 never fed on *V. felis* directly.

Modes of Predation

Three modes of predation have been reported in gymnodorids: biting the prey, swallowing it whole, and sucking the body fluid from the prey (Hughes, 1983; Johnson, 1992; Ono, 1999, 2004; Nakano, 2004; Behrens, 2005; Nakano et al., 2007). We did not observe sucking behavior. After capturing the prey

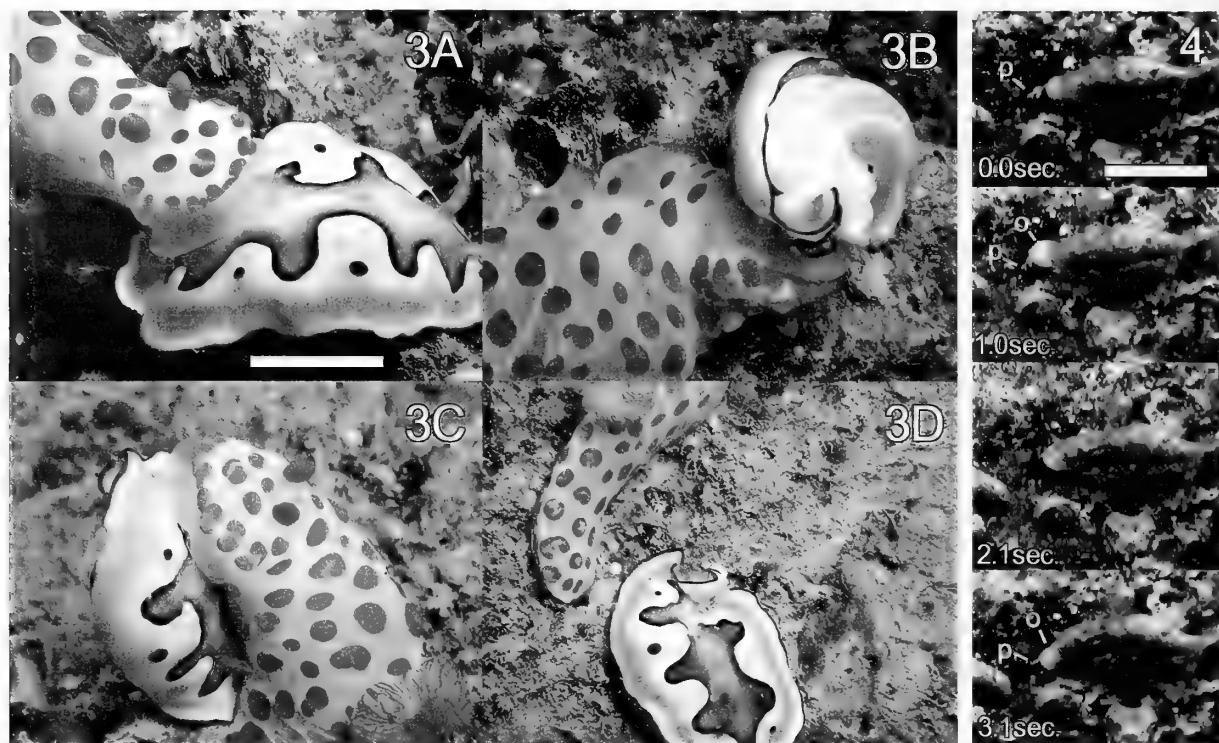


Figure 3. *Gymnodoris rubropapulosa* shook its *Chromodoris coi* prey to bite off the dorsal part. Scale bar = 10 mm.

Figure 4. *Gymnodoris* sp. B grasping a prey (p), *Thuridilla vatae*, with the radula (o) on the odontophore (o). The predator repeatedly extended and retracted the odontophore three times within 9 sec to drag the prey into the esophagus. The images were captured from a video. Scale bar = 10 mm.

with the buccal apparatus, the gymnodorids we observed bit but did not feed on the prey, bit off part of the prey and fed on it partly, or completely devoured the prey.

Gymnodoris okinawae swallowed several *Elysia* species whole, but not *E. lobata* Gould, 1852 and *Elysia* sp. B. When we offered *E. lobata* to *G. okinawae* No. 3, the predator bit off part of the prey, leaving the head. *Elysia* sp. B, known by its Japanese common name "tsunokuro-midorigai" (cf. Ono, 2004), is an undescribed species that is commonly found in southern parts of Japan. When we offered *Elysia* sp. B to *G. okinawae* No. 5, the predator cut off the parapodia of the prey (Figure 2) and swallowed them, but the wounded prey animal, with head and foot, including the pericardium, intact then escaped.

Two *G. rubropapulosa* individuals fed on *Chromodoris aureopurpurea* Collingwood, 1881 and *C. coi* (Risbec, 1956), respectively. In both cases, the predators did not completely swallow their prey. *Gymnodoris rubropapulosa* No. 1 bit *C. aureopurpurea* on its dorsal side and tried to swallow it. About 8 minutes later, *G. rubropapulosa* No. 1 shook the prey, and 13 minutes later, the predator bit off a portion of the prey. The mantle of *C. aureopurpurea* was partly damaged, and

the animal had already died. *Gymnodoris rubropapulosa* No. 2 bit *C. coi* on its dorsal side and immediately shook the prey. Fourteen minutes later, the predator bit off part of the prey. Although the mantle of *C. coi* was partly damaged, the prey was still alive (Figure 3).

To feed, *Gymnodoris* sp. B extended its large odontophore from the mouth to grasp the prey with its radula and then retracted the odontophore to drag the prey into its esophagus. The predator repeated the extension and retraction of the odontophore three times within 9 sec, until the prey was dragged into the esophagus (Figure 4).

DISCUSSION

Of the gymnodorids that feed on nudibranchs of various orders, some feed exclusively on particular groups (Kay & Young, 1969; Kay, 1979; Johnson & Boucher, 1983; Hughes, 1983; Johnson, 1992; Behrens, 2005; Nakano et al., 2007). Our *in situ* observations are basically consistent with previous records. However, we note that laboratory experiments may produce abnormal feeding behavior in predators. The unique food habits of gymnodorids will be revealed by the repetition and accumulation of field experiments, using as many species and individuals as possible.

Our study showed that some individuals of *G. alba*, *G. citrina*, *G. okinawae*, and *Gymnodoris* sp. B are occasionally able to locate a mucus trail and pursue their prey before direct contact with the prey, whereas the other individuals of the above four species and all the individuals of *G. rubropapulosa* do not recognize the prey until they touch them (see Table 2). Although gymnodorids are known to swallow their prey whole or suck its body fluids (Young, 1969; Hughes, 1983; Johnson, 1992; Ono, 1999, 2004; Nakano, 2004; Behrens, 2005; Nakano et al., 2007), we found that some predators bit off parts of the prey. In these cases, the predator did not eat the prey completely, and one prey individual escaped without its parapodia. Biting off pieces rather than complete ingestion may be related to body size of prey. It is also possible that the predator chooses to bite off prey when the prey is an unusual prey species for the predator and/or the predator is not hungry. We did not observe sucking behavior in the present study.

Kay & Young (1969), Kay (1979), and Hughes (1983) reported that in the laboratory *G. alba* feeds on several species of the suborder Aeolidina, as did Takasaki, Natani, Hoson, and Matsuda (personal communications), who observed *G. alba* in the field feeding on *Phidiana indica* (Bergh, 1896), *Cratena lineata* (Eliot, 1905), and an undescribed aeolidinan. The undescribed aeolidinan is conspecific to Aeolidina sp. 24 (No. 658) in Nakano (2004). In this study, we observed *G. alba* feeding on *Vayssiarea felis* (Nudibranchia: Doridina: Vayssiareidae) and its eggs. *Vayssiarea felis* is a small nudibranch (~3 mm long) that inhabits intertidal and subtidal zones of rocky shores in Japan. It is much smaller than the aeolidinans and moves very slowly. Occasionally, we found many *V. felis* in one location. Thus, *V. felis* would be an easily obtainable prey species for *G. alba* that inhabit intertidal and subtidal zones. However, since the habitat of *V. felis* is very restricted, *G. alba* inhabiting deeper sites would not encounter this prey species. As the external features of *G. alba* feeding on *V. felis* and that feeding on an aeolidinan do not differ, we conclude that *G. alba* feed on both *V. felis* and aeolidinans, depending on the habitat.

Gymnodoris okinawae are known to feed on *Elysia* spp. and an undescribed *Thuridilla* sp. (Kay & Young, 1969; Young, 1969; Johnson & Boucher, 1983; Nakano et al., 2007). This undescribed *Thuridilla* species is commonly found in southern Japan and is known by its Japanese common name, “fujiro-midorigai” (see Ono, 2004). Unfortunately, we could not test “fujiro-midorigai” as a prey candidate for *G. okinawae* in this study. We observed *G. okinawae* attacking and severing the parapodia of *Elysia* sp. B. This undescribed *Elysia* species is commonly found in southern Japan and is known by its Japanese common name, “tsunokuro-

midorigai” (see Ono, 2004). While *G. okinawae* fed on the parapodia, the prey escaped. We still do not know whether this was a type of autotomy on the part of *Elysia* sp. B. Moreover, we observed that *G. okinawae* fed on *Metaruncina setoensis* (Cephalaspidea: Runciniidae), which is a small cephalaspidian (~5 mm long) inhabiting the rocky shores of Japan from the intertidal to the subtidal zones. *Metaruncina setoensis* is much smaller than *Elysia*, moves very slowly, and is often abundant in some locations. As the external morphology of *G. okinawae* feeding on *M. setoensis* does not differ from that feeding on *Elysia* spp. we conclude that *G. okinawae* feeds on both *M. setoensis* and *Elysia* species. Johnson & Boucher (1983) reported that *G. okinawae* fed on a cephalaspidian, which was probably *M. setoensis* or another runcinid closely related to *M. setoensis*.

The feeding behavior of *G. citrina* is unique; this carnivore feeds not only on congeners and their eggs, but also on conspecifics (Johnson, 1992; Nakano et al., 2007). Although we offered 23 opisthobranch individuals (21 species) to seven *G. citrina* individuals as prey candidates, including *Gastropteron* sp. (Cephalaspidea: Gastropteridae), *Elysia* sp. (Sacoglossa), *Vayssiarea felis* (Nudibranchia: Doridina), and *Baeolidia japonica* Baba, 1933, (Nudibranchia: Aeolidina), *G. citrina* fed exclusively on gymnodorids (*G. alba*, *G. citrina*, and *G. okinawae*) and was not interested in any of the other prey candidates. Our results were consistent with previous reports (Young, 1969; Johnson & Boucher, 1983; Johnson, 1992; Nakano et al., 2007). *Gymnodoris citrina* No. 3 chased and touched *Hexabranchius sanguineus* (Rüppell & Leuckart, 1828) but did not feed on it. Although it is uncertain why this *G. citrina* pursued the nongymnodorid, some possible explanations include: (1) *H. sanguineus* was not the prey item, and *G. citrina* was following another mucus trail that coincidentally ran along that of *H. sanguineus*; (2) *H. sanguineus* is a prey species, but the predator had just eaten *G. okinawae* and was full; (3) *H. sanguineus* is not a prey species, but its mucus trail contains signals similar to those of *G. citrina* prey.

Nakano et al. (2007) reported from field observations that *G. rubropapulosa* swallowed *Chromodoris strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata* whole. The undescribed *Chromodoris* species is commonly found in the vicinity of Hachijo-jima Island and the Bonin Islands, and is known by its Japanese common name, “kongasuri-umiushi” (see Nakano, 2004). This predator also feeds on *G. rufomarginata* (Bergh, 1890), *Hypselodoris iacula*, *H. dollfusi* (Pruvot-Fol, 1933), *H. krakatoa* Gosliner & Johnson, 1999 and *M. marieri* (Crosse, 1872) (Behrens, 2005; Behrens, personal communication). These observations suggest that *G. rubropapulosa* feeds on chromodoridid family members, usually by swallowing its

prey whole. We observed *G. rubropapulosa* feeding on two other *Chromodoris* species: *C. aureopurpurea* and *C. coi*. However, neither of two *G. rubropapulosa* individuals swallowed their prey, but bit off portions of it within a few minutes. These prey animals (ca. 30 mm) were probably too large for the predators (ca. 80 mm) to swallow. Thus, *G. rubropapulosa* may change its mode of feeding depending on prey size and/or species.

In this study, we discriminate *Gymnodoris* sp. B from *G. alba* based on the difference their body colors. If *Gymnodoris* sp. B were a color morph type of *G. alba*, it should feed on *Vayssierea felis* or species of the suborder Aeolidina. Unfortunately, we were not able to offer it these prey candidates. However, the prey species of *Gymnodoris* sp. B were more similar to those of *G. okinawae* than those of *G. alba*. As described above, *G. okinawae* feeds on *Elysia* spp. but not *Thuridilla* spp. with one exception. In our study, *G. okinawae* ignored *T. vatae*. However, it does feed on *Thuridilla* sp. which is known in Japan as “fujiirō-midorigai.” Both *Elysia* and *Thuridilla* belong to the family Elysiidae (Elysiodea). The four *Gymnodoris* sp. B individuals in our study ate *T. vatae* and some *Elysia* species, but not other *Thuridilla* spp., e.g., *T. katae* Gosliner, 1995, *T. splendens* (Baba, 1949), *T. gracilis* (Risbec, 1928) and *T. albopustulosa* Gosliner, 1995. This observation suggests that *Gymnodoris* sp. B differs from *G. okinawae* in its food habits as well as its morphology. Kay & Young (1969) reported that the genital orifice of *G. okinawae* is immediately posterior to the cephalic hood, but we observed it to be halfway between the cephalic hood and the gill. Moreover, the genital orifice of *G. okinawae* is small and inconspicuous. Body colors also discriminate *G. okinawae* from *Gymnodoris* sp. B. Thus, *Gymnodoris* sp. B appears to be an undescribed species, although detailed observations, including internal morphology, are necessary to clarify the taxonomic status of this gymnodorid.

Among the 21 predatory gymnodorid individuals we examined, only *G. citrina* No. 7 located prey at an 80-mm distance. When the predator almost lost the mucus trail of its prey, it raised the upper part of its body and swung its head until it located the mucus trail again. Similar behavior was reported for *Navanax inermis*: “If the trail is chased away from the prey, a characteristic ‘searching’ behavior is observed at its end. Once contact is lost, *Navanax* swings its head back and forth in small arcs, and eventually may even turn itself around” (Paine, 1963). The *N. inermis* experiment was conducted in a shallow aquarium with a flat sandy bottom, whereas our experiments were conducted in the field at a depth of 2 m. Therefore, the different experimental conditions possibly caused some differences in the feeding behaviors. Alternatively, the two very distantly related opisthobranchs may exhibit different behaviors. Opisthobranchs that feed on

opisthobranchs, such as *N. inermis* and *Gymnodoris*, may use chemoreception to locate and chase their prey. The head-swinging behavior of both *N. inermis* and *G. citrina* suggests that these predators perceive diffusible molecules released from the mucus trail and/or the body surface of the prey.

In our study, gymnodorids did not always locate and chase prey effectively. Since both *Gymnodoris* spp. and their prey crawl slowly, we are not sure how they find sufficient prey to survive. Some predators seem to process chemical cues from their prey; however, the cue molecules and reception mechanism(s) of gymnodorids remain to be elucidated.

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Fossil *Adulomya* (Vesicomysidae, Bivalvia) from Japan

KAZUTAKA AMANO

Department of Geosciences, Joetsu University of Education, Joetsu 943-8512, Japan
(e-mail: amano@juen.ac.jp)

AND

STEFFEN KIEL

Department of Geobiology, University of Göttingen, Göttingen 37077, Germany

Abstract. The Cenozoic fossil record of the vesicomysid bivalve genus *Adulomya* in Japan is evaluated. Five of the nominal species are confirmed based on shell morphology, hinge dentition, and the shape of the pallial line. Two of these are new to science: *Adulomya hamuroi* sp. nov. from the uppermost lower or lowest middle Miocene Higashibessho Formation in Honshu, and *Adulomya kuroiwaensis* sp. nov. from the uppermost middle or lowest upper Miocene Ogaya Formation in Honshu. A well-preserved specimen of *Adulomya uchimuraensis*, the type species of *Adulomya*, shows that this species lacks a pallial sinus and has an elongate ovate posterior adductor muscle scar. We redescribe *Adulomya chitanii* based on well-preserved, newly collected material. The identity of specimens previously assigned to the latter two species is outlined. *Adulomya* appears to have dispersed during the early Miocene from western North America along the North Pacific continental slope to Japan. It is present with five species in early and middle Miocene strata of Japan and shows a steep decline in diversity through the late Miocene and Pliocene. This decline coincides with, and may thus be linked to, the appearance and diversification of the vesicomysid genera *Archivesica* and *Calyptogena* from the late Miocene onwards. In the waters around Japan today, species of *Adulomya* live in deeper water than other vesicomysids and might thus have followed the onshore–offshore trend as suggested for other members of the vent and seep fauna.

INTRODUCTION

Vesicomysid bivalves are among the more prominent members of the chemosynthetic deep-sea fauna and have been frequently recorded from the Cenozoic fossil record of Japan (Amano & Kanno, 2005; Majima et al., 2005). These species were described under various generic names including *Calyptogena* Dall, 1891; *Adulomya* Kuroda, 1931; *Akebiconcha* Kuroda, 1943; *Hubertschenckia* Takeda, 1953; and *Vesicomys* Dall, 1886 (Hatai & Nisiyama, 1952; Masuda & Noda, 1976; Nobuhara, 2003). A revised generic classification of vesicomysid bivalves from the North Pacific region has recently been established (Amano & Kiel, 2007). Accordingly, the large-sized vesicomysids in this region can be assigned to the following four genera: *Calyptogena*; *Archivesica* Dall, 1908; *Adulomya*; and *Hubertschenckia* (Table 1).

Among these, *Adulomya* includes elongate to very elongate shells with a very small or no pallial sinus, and with only two cardinal teeth in the right valve instead of three, as in most other vesicomysids. Fossil species in Japan include the long-known *Adulomya uchimuraensis* Kuroda, 1931, *Adulomya chitanii* Kanehara, 1937, and the recently established *Adulomya hokkaidoensis* Amano & Kiel, 2007. The former two names have

been assigned to many Mio-Pliocene specimens, often based merely on the general shell outline. Whereas the characteristics of *A. uchimuraensis* have been described in detail (Kanno et al., 1998), the features of *A. chitanii* are insufficiently known or have been confused with those of other species (e.g., the ‘ontogenetic change’ of Kanno, 1971). Based on newly collected material and investigations of museum material, we provide here a detailed description of *A. chitanii*, describe two new species of *Adulomya*, outline the status of other species described as or assignable to *Adulomya*, and discuss the evolutionary implications of our findings.

MATERIAL

New material was collected from four Miocene and Pliocene formations in Honshu (Figure 1). Specimens of the type species of *Adulomya*, *A. uchimuraensis*, were collected from isolated carbonate bodies embedded in black mudstone of the middle Miocene Bessho Formation at Akanuda in Nagano Prefecture (Figure 1, loc. 1).

New material of *A. chitanii* was collected from isolated carbonate bodies within the Taira Formation at Donosaku, Iwaki City, in Fukushima Prefecture (= loc. 8 of Aoki, 1954; Figure 1, loc. 2 herein). Aoki

Table 1
Characteristics of the vesicomysid genera.

+ present; – absent; ± basically absent, but sometimes present.

Genus	Maximum size (mm)	Subumbonal pit*	Pallial sinus**	Elongate shell	3a tooth	Nymphal ridge
<i>Adulomya</i>	180	±	±	+	–	–
<i>Archivesica</i>	250	+	+	±	+	–
<i>Hubertschenckia</i>	75	+	+	–	+	+
<i>Calyptogena</i>	90	–	–	±	+	+

* Krylova & Sahling (2006) pointed out that *Ectenagena* (= *Adulomya*) has a subumbonal pit. However, other than *A. elongata*, this genus does not have a distinct subumbonal pit. Amano & Kiel (2007) mistakenly illustrated a subumbonal pit in *Calyptogena* of their fig. 5, but this genus does not have it.

** While Krylova & Sahling (2006) showed that *Ectenagena* (= *Adulomya*) lacks a pallial sinus, *A. phaseoliformis* and *A. chitanii* show a v-shaped pallial sinus as described in the text.

(1954) reported the vesicomysid *Vesicomys kawadai* from the same outcrops.

Elongate vesicomysids were collected from turbidite deposits of the uppermost lower or lowest middle Miocene Higashibessho Formation at Shimo-Sasahara (Figure 1, loc. 3), Toyama City, in Toyama Prefecture. Vesicomysid specimens from this locality had previously been described as *Calyptogena* sp., (Amano et al., 2001).

Further elongate vesicomysids were extracted from isolated carbonate bodies within the upper Miocene Ogaya Formation at Kuroiwa (Figure 1, loc. 4), Joetsu City in Niigata Prefecture. Vesicomysid specimens from this locality had previously been described as *Calyptogena* sp. B by Amano & Kanno (2005).

All newly collected material is housed in the Joetsu University of Education (JUE). In addition, we examined specimens identified as *A. uchimuraensis* from the lower Miocene Nabae Group at Muroto (Figure 1, loc. 5) in Kochi Prefecture, Shikoku, which are housed at the National Science Museum (NSM) (Matsumoto & Hirata, 1972); and specimens of '*Calyptogena*' *akanudaensis* Tanaka, 1959 from the middle Miocene Bessho Formation in Nagano Prefecture, housed at the Shinshu-Shinmachi Museum.

SYSTEMATIC DESCRIPTIONS

Family VESICOMYIDAE Dall & Simpson, 1901

Genus *Adulomya* Kuroda, 1931

Type species: *Adulomya uchimuraensis* Kuroda, 1931, from the middle Miocene Bessho Formation, central Honshu, Japan.

Remarks: Kanno et al. (1998) redescribed the type species in detail. *Adulomya* is characterized by its elongate shape, having two radiating cardinal teeth in the right valve; a pallial sinus is lacking except for *A.*

chitanii and *Adulomya phaseoliformis* Metivier, Okutani & Ohta, 1986, where the pallial line starts from the central part of posterior adductor muscle scar and forms a v-shaped pallial sinus (see also Amano & Kiel, 2007). Some of these characters can also be found in the enigmatic genus *Pleurophopsis*. Its type species, however, is too poorly preserved to show all characters needed for a robust classification and should thus not be used (Kiel, 2007).

Adulomya uchimuraensis Kuroda, 1931

(Figure 2)

Adulomya uchimuraensis Kuroda, 1931:27–28, pl. 13, figs. 111–114; Tanaka, 1959:117–118, pl. 1, fig.1–10; Tanaka, 1960:24–26, pl. 32, figs.1–7.

Calyptogena (Adulomya) uchimuraensis Kuroda. Kanno & Tanaka in Kanno et al., 1998:20–22, figs. 7–8.

Calyptogena (Adulomya) uchimuraensis kurodai Kanno & Tanaka in Kanno et al., 1998:22–25, figs. 9–10.

Akebiconcha chitanii (Kanehara). Kanno & Ogawa, 1964:pl.1, figs. 17–18.

? *Adulomya uchimuraensis* Kuroda. Hayashi & Miura, 1973:pl. 1, fig. 15.

non-Akebiconcha uchimuraensis Kuroda. Matsumoto & Hirata, 1972:755–757, pl. 1, figs. 1–8, pl. 2, figs. 1–2.

Type material: According to Hatai & Nisiyama (1952), the type material is housed in the Institute of Geology and Mineralogy, Faculty of Science, Hokkaido University. Their register numbers, however, are unknown.

Material examined: Twenty-seven specimens from loc. 1 were examined. Among them, five specimens are well preserved and were measured (Table 2).

Remarks: In their redescription of *A. uchimuraensis*, Kanno et al. (1998) described the pallial sinus and

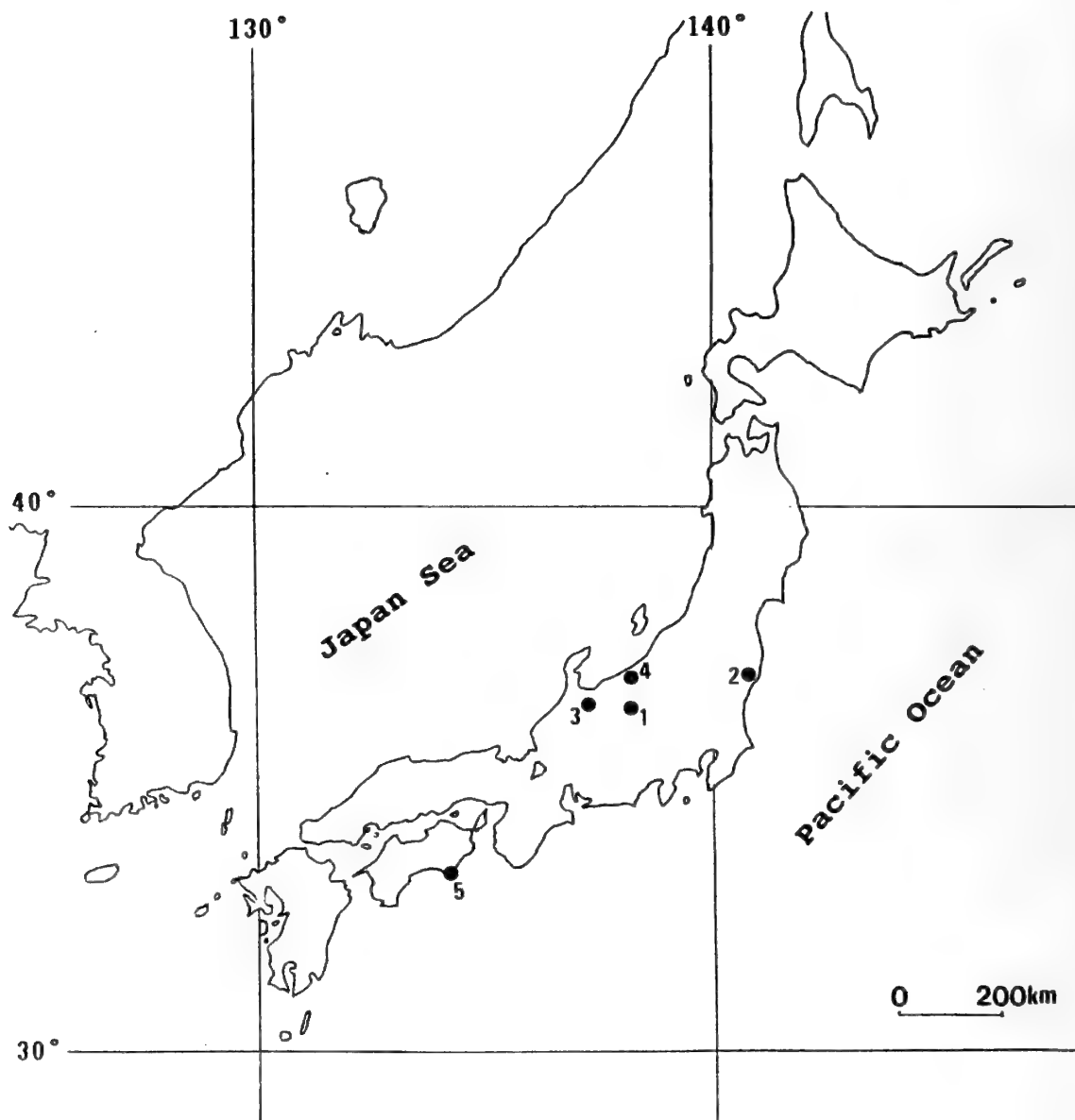


Figure 1. Locality maps of fossil specimens. Numbers of localities are shown in the text.

posterior adductor scar as indistinct and obscure, respectively. A newly collected well-preserved specimen (Figure 2) shows no pallial sinus and an elongate ovate posterior adductor muscle scar as present in most species of *Adulomya*. As already suggested by Amano & Kiel (2007), the subspecies *Calypptogena (Adulomya) uchimuraensis kurodai* Kanno & Tanaka in Kanno et al. (1998) is a synonym of *A. uchimuraensis*. According to Kanno et al. (1998) this “subspecies” differs from *A.*

uchimuraensis sensu strictu by having a straight ventral margin, and a higher and less convex shell. Our material does not show these differences in juvenile (= small) specimens, and we have transitional forms that are intermediate between the two putative subspecies.

Specimens that most likely belong to *A. uchimuraensis* were reported by Kanno & Ogawa (1964) as *Akebiconcha chitanii* from the lowest middle Miocene

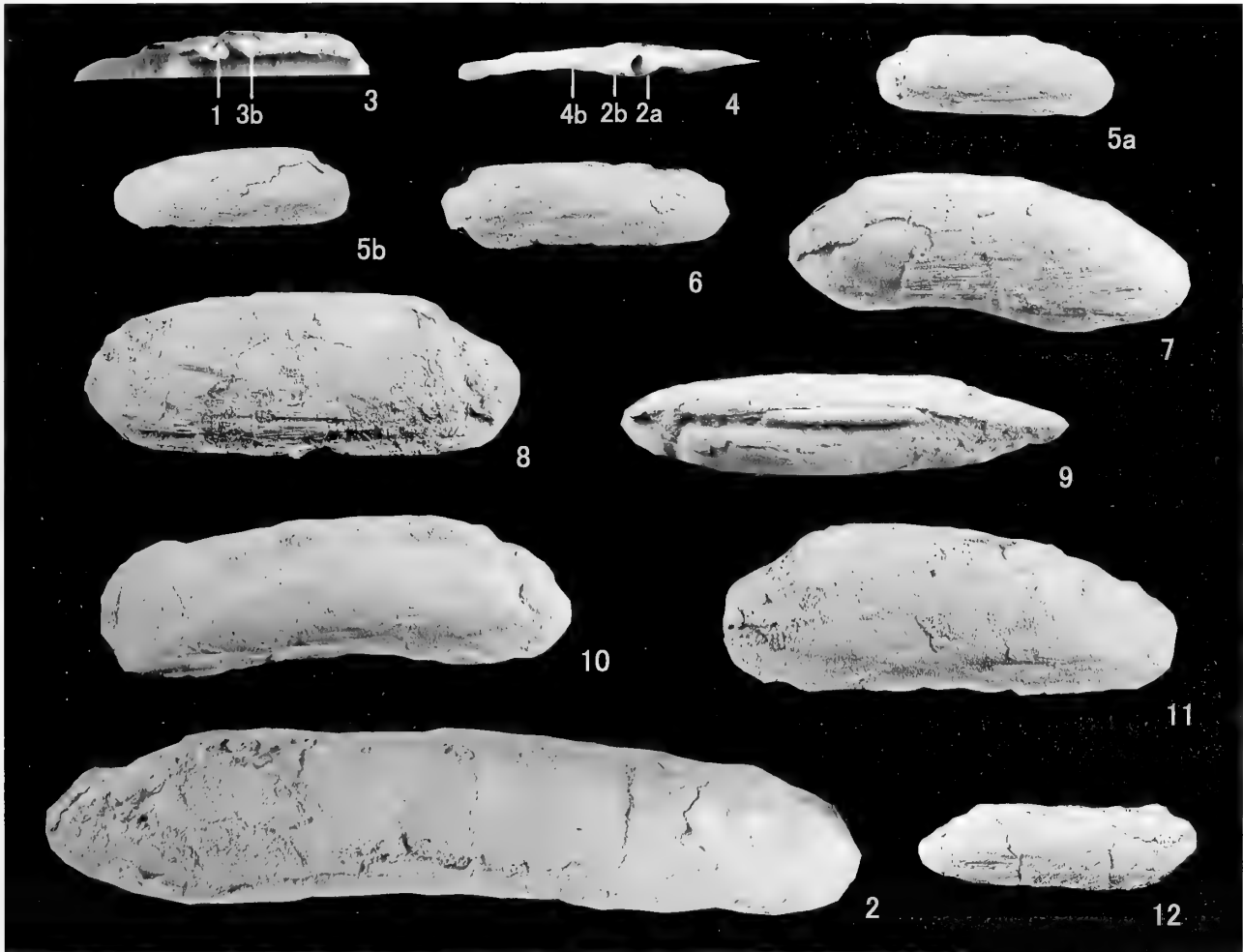


Figure 2. *Adulomya uchimuraensis* (Kuroda). Left valve showing the posterior adductor muscle scar and the entire pallial line; length 94.3 mm, JUE no. 15865-1, loc. 1.
Figures 3–12. *Adulomya chitanii* (Kanehara). All specimens are from loc. 2. Figure 3. Right-valve hinge, hinge length 15.4 mm, JUE no. 15866-29. Figure 4. Left-valve hinge, hinge length 19.4 mm, JUE no. 15866-30. Figures 5–6, 12. Outline of juvenile shells; Figure 5a,b, length 32.9 mm, JUE no. 15866-25; Figure 6, length 39.7 mm, JUE no. 15866-26; Figure 12, length 38.3 mm, JUE no. 15866-27. Figures 7–9. Outline of adult shells; Figure 7, length 55.5 mm, JUE no. 15866-23; Figure 8, length 61.0 mm, JUE no. 15866-8; Figure 9, dorsal view showing long external ligament, length 61.9 mm, JUE no. 15866-28. Figures 10–11. Pallial sinus of both valves; Figure 10, length 66.5 mm, JUE no. 15866-21; Figure 11, length 62.4 mm, JUE no. 15866-3.

Table 2
Measurements of *A. uchimuraensis*
(Kuroda) from loc. 1.

JUE specimen no.	Length (mm)	Height (mm)	Valve
15865-1	94.3	19.5	left
15865-2	91.3	20.9	left
15865-3	111.3	26.6	left
15865-4	120.5	27.5	right
15865-5	94.3	18.9	left

Takinoue Formation in Hokkaido. These specimens have longer and lower shells (length ca. 69 mm, height 16 mm) than *A. chitanii* and, in contrast to *A. chitanii*, lack a pallial sinus (see below).
Matsumoto & Hirata (1972) recorded *Akebiconcha uchimuraensis* from the Nabae Group in Shikoku. The age of the sediments was considered as late Oligocene, but recent micropaleontological work showed that they were deposited during the early Miocene (Iijima et al., 1981; Okamura & Taira, 1984; Suyari et al., 1989). The hinge dentition could not be investigated in any of the available specimens. However, specimens from the Nabae Group have an elongate shell with concave

ventral margin as shown in Figures 30 and 31. The largest specimen (i.e., Figure 31b) reaches 112.5 mm in length, has a distinct ridge just anterior to the ovate posterior adductor muscle scar, and lacks a pallial sinus. It might thus belong to *Adulomya*, although this needs to be confirmed by data on its hinge dentition. It differs from *A. uchimuraensis* by having a smaller and higher adult shell, a truncated anterior margin, and a deeply concave ventral margin unlike that of *A. uchimuraensis*.

Hayashi & Miura (1973) illustrated an elongate shell from the Miocene Okazaki Formation as *A. uchimuraensis*, but its hinge dentition and pallial line are unknown and thus its identity remains unclear.

Comparison: *Adulomya uchimuraensis* is similar to the Recent *A. phaseoliformis* in size and shell outline but differs by lacking a pallial sinus.

Distribution: Middle Miocene Bessho Formation in Nagano Prefecture and lowest middle Miocene Takinoue Formation in Hokkaido.

Paleobathymetry: Kanno et al. (1998) estimated that the sediments of the Bessho Formation at Akanuda were deposited in less than 200 m depth, based on the associated molluscan fossils. Kanno & Ogawa (1964) reported *Portlandia* cf. *tokunagai* and *Bathymalletia inermis* as the associated fauna of *A. chitanii* (= *A. uchimuraensis*) from the Takinoue Formation in Hokkaido. Extant members of these genera are found between the lower sublittoral and the middle bathyal zone (Higo et al., 1999). Thus, *A. uchimuraensis* most likely lived in this depth range, too.

Adulomya chitanii Kanehara, 1937

(Figures 3–12)

Adulomya chitanii Kanehara, 1937:19–20, pl. 5, figs. 1, 6–9; Kamada, 1962:39–41, pl. 1, figs. 4–7.

"*Adulomya*" *chitanii* Kanehara. Aoki, 1954:31–32, pl. 1, figs. 9–11.

Calypptogena chitanii (Kanehara). Kanno & Akatsu, 1972:pl. 8, figs. 13, 14; Amano & Little, 2005:figs. 6B, 6C, 6D; Amano & Jenkins, 2007:fig. 2C; Amano et al., 2007:figs. 3C, 3F, 3H.

Calypptogena sp., Yamaoka, 1993:pl. 4, figs. 1, 6, 7.

? *Calypptogena chitanii* (Kanehara). Shikama & Kase, 1976:pl. 2, fig. 6; Hirayama, 1973:175, pl. 15, fig. 12–13; Yamaoka, 1993:pl.4, figs. 2, 3.

? *Akebiconcha chitanii* (Kanehara). Hayashi & Miura, 1973:pl. 1, fig. 26; Hayashi, 1973: pl. 5, fig. 6.

non-Akebiconcha chitanii (Kanehara). Kanno & Ogawa, 1964:pl. 1, figs. 17–18; Kanno & Arai, 1964:pl. 1, figs. 19–22; Kanno, 1967:401–402, pl. 1, figs. 9–11, 15.

Table 3
Measurements of *A. chitanii*
(Kanehara) from loc. 2.

JUE specimen no.	Length (mm)	Height (mm)	Thickness (mm)
15866-1	70.4	21.0	13.7
15866-2	62.6	19.7	17.1
15866-3	62.4	21.8	14.7
15866-4	67.1	22.0	15.5
15866-5	61.7	19.6	14.2
15866-6	63.1	20.2	17.1
15866-7	57.9	17.0	11.5
15866-8	61.0	22.2	14.8
15866-9	67.1	21.1	13.6
15866-10	56.4	18.0	11.9
15866-11	58.8	19.5	17.0
15866-12	53.3	18.9	14.7
15866-13	55.2	18.7	14.2
15866-14	54.7	16.8	13.8
15866-15	53.3	19.8	12.8
15866-16	52.8	17.0	10.2
15866-17	54.3	17.1	10.5
15866-18	43.9	14.5	10.1
15866-19	48.6	14.9	9.0
15866-20	45.1	15.2	10.1
15866-21	66.5	19.8	14.0
15866-22	60.6	19.0	15.8
15866-23	55.5	17.9	—
15866-24	66.3	22.5	—
15866-25	32.9	10.6	5.9
15866-26	39.7	11.9	8.1
15866-27	38.3	11.4	7.4
15866-28	61.9	21.3	—

non-Calypptogena chitanii (Kanehara). Kanno, 1971:80–82, pl. 7, figs. 5–6.

Type material: Kanehara's (1937) type material from the Mizunoya Formation was destroyed during World War II (Hatai and Nisiyama, 1952; Kamada, 1962) and a neotype has never been assigned. Here we designate the specimen illustrated by Kamada (1962:pl. 1 fig. 4 = Amano & Jenkins, 2007:fig. 2C) stored at Institute of Geology and Paleontology, Tohoku University (IGPS no. 87339) as neotype.

Material examined: Twenty-seven well-preserved specimens from loc. 2 (Table 3) and the four specimens illustrated by Kamada (1962).

Supplementary description: Shell small for genus, up to 70.4 mm long, thin-walled, elongate throughout ontogeny (height/length ratio = 0.29–0.37), equivalve and inequilateral, weakly inflated, sculptured only by growth lines. Beak prosogyrate, situated at anterior one-eighth of shell length in juvenile specimens and at one-fifth in adults. Anterodorsal margin broadly arched, graduating into narrowly rounded anterior margin; ventral margin straight or slightly concave;

posterodorsal margin nearly straight, parallel to ventral margin, graduating into rounded posterior margin. Escutcheon and lunule absent; ligament exterior, strong and long, occupying three-fifths of posterodorsal margin.

Hinge plate narrow, with two cardinals in right valve and three cardinals in left valve. Right valve hinge: anterior cardinal tooth (3a) reduced; posterior cardinal tooth (3b) slightly bifid, oblique posteriorly; central tooth (1) thin, vertical to hinge base; subumbonal pit absent. Left valve hinge: anterior tooth (2a) thin, slightly oblique anteriorly, connected to stout middle tooth (2b); posterior tooth (4b) thin, oblique posteriorly; subumbonal pit absent. Nymph distinct and long, occupying two-thirds of the posterodorsal margin.

Anterior adductor muscle scar subcircular; posterior one ovate; pallial sinus very shallow and v-shaped; distinct inner ridge running from just under the posterior muscle scar to umbo; radial interior indistinct.

Remarks: There are numerous records of *A. chitanii* from lower to middle Miocene strata in Japan and Alaska. Many of these identifications are based only on external morphology and their identity is doubtful. This concerns records (as *Calyptogena chitanii* or *Akebiconcha chitanii*) from the Morozaki Group by Shikama & Kase (1976) and Yamaoka (1993), from the Okazaki Formation by Hayashi & Miura (1973), from the Ohno Formation in Aichi Prefecture by Hayashi (1973), and from the Hiranita Formation in Saitama Prefecture by Hirayama (1973).

In addition to the insufficient original description of Kanehara (1937), Kanno (1971) presented a scheme of the ontogenetic morphological change of this species that we are unable to confirm and that might have led to further confusion: elongate-ovate specimens described from the Itsukaichimachi Group in Tokyo Prefecture by Kanno & Arai (1964) and Kanno (1967) were considered juvenile forms, and Kanno's (1971) Alaskan specimens with large elongate shells and a concave ventral margin were considered adults (Kanno, 1971:text, fig. 11). Our observations of *A. chitanii* from loc. 2, however, indicate that juveniles and adults of *A. chitanii* have very similar proportions and the ventral margin is not as strongly concave as in the Alaskan specimens figured by Kanno (1971:pl. 7, fig. 6). Considering its two cardinal teeth and elongate shape, Kanno's Alaskan species belongs to *Adulomya* but not to *A. chitanii* (see also Kiel and Amano, 2010). Masuda & Noda (1976) suggested that specimens reported by Kanno & Arai (1964) and Kanno (1967) from the Itsukaichimachi Group belong to *Calyptogena pacifica*. However, the illustration of a right valve (Kanno & Arai, 1964:pl. 1, fig. 22; Kanno, 1967:pl. 1, fig. 15) shows two small cardinal teeth whereas *Calyptogena pacifica* has three. The specimens from the Itsukaichi-

machi Group might thus belong to *Adulomya*, but can currently not be assigned to any known species.

Comparison: *Adulomya chitanii* and *A. uchimuraensis* have been confused in the past, but can be easily distinguished by the lack of a pallial sinus in *A. uchimuraensis*, whereas it is present in *A. chitanii*. In addition, *A. uchimuraensis* grew to about 180 mm in length and has lower shell (height/length ratio = 0.12–0.26) whereas the maximum size of *A. chitanii* is about 70 mm and its height/length ratio ranges from 0.29 to 0.37.

Distribution: Lower Miocene Mizunoya, Kamenoo, and Taira Formations in Fukushima Prefecture; lower Miocene Toyohama Formation of Morozaki Group in Aichi Prefecture; middle Miocene Nupinai Formation in eastern Hokkaido.

Paleobathymetry: Taketani et al. (1990) used foraminifera to estimate that the Mizunoya, Kamenoo, and Taira formations were deposited in sublittoral to middle bathyal depth. The depositional depth of the Morozaki Group was estimated to range from 100 to 600 m by Shikama & Kase (1976). From the Nupinai Formation, Kanno & Akatsu (1972) listed *Portlandia*, *Nuculana*, *Periploma*, *Turritella*, and *Olivella*; based on the bathymetric range of living members of these genera (cf. Higo et al., 1999), the Nupinai Formation was deposited between the lower sublittoral and the upper bathyal zone. Thus, the bathymetric range of *A. chitanii* was probably from the lower sublittoral to the middle bathyal zone.

Adulomya hokkaidoensis Amano & Kiel, 2007

Calyptogena sp., Amano & Little, 2005:figs. 5 A, E, F.
Adulomya hokkaidoensis Amano & Kiel, 2007:278, figs. 13–18.

Type material: JUE no. 15848 (holotype) and JUE no. 15849 and 15850 (paratype) from the lower middle Miocene Chikubetsu Formation (upper part) in north-western Hokkaido.

Distribution: Known only from the whale-fall community at the type locality.

Paleobathymetry: Benthic foraminifera suggest that *A. hokkaidoensis* lived at depth below the middle bathyal zone (cf. Maiya et al., 1982).

Adulomya hamuroi Amano & Kiel, sp. nov.

(Figures 13–17)

Calyptogena sp., Amano et al., 2001:192, 194, figs. 6–7, 12–14.

Diagnosis: A medium-sized *Adulomya* with elongate trapezoidal or elliptical shell having a concave ventral margin, and sculptured by fine growth lines. Right valve with two cardinal teeth: a stout and bifid posterior cardinal (3b) and an anterior cardinal (1) perpendicular to hinge base; no subumbonal pit; left valve with three cardinal teeth: short anterior cardinal (2a), stout and posteriorly oblique central cardinal (2b), and thin and long posterior cardinal (4b).

Holotype: Length 49.9 mm, height 23.3 mm, JUE no. 15857.

Paratypes: Length 36.3 mm, height 24.4 mm, JUE no. 15698-1; length 37.5 mm, height 26.6 mm, JUE no. 15698-2; length 59.2 mm, height 22.3 mm, JUE no. 15698-6.

Type locality: A large cliff about 250 m west of Shimosahara, Yatsuo Town, in Toyama City, Toyama Prefecture; uppermost lower or lowest middle Miocene Higashibessho Formation.

Description: Shell thin, medium-sized (up to 59.2 mm in length), elongate-trapezoidal or elliptical, equivalve and inequilateral. Anterodorsal margin broadly arcuate; posterodorsal margin long, almost straight nearly parallel to ventral margin; ventral margin slightly concave in its central part. Beak very low, prosogyrate, and situated at anterior one-fifth of entire shell length. Surface sculptured by irregularly spaced growth lines; lunule absent; escutcheon not clearly demarcated. Nymph plate long and raised slightly above dorsal margin. Hinge plate narrow with two radiating teeth in each valve; no subumbonal pit. Right valve with strong, triangular anterior cardinal (1) starting below umbo and pointing downward, posterior cardinal (3b) equally strong, fused with anterior cardinal, bifurcating at posterior end, short, almost parallel to dorsal margin. Left valve with small anterior cardinal (2a) not reaching hinge base; central cardinal (2b) bifid with widely gaping edges; posterior cardinal (4b) long and thin. Both anterior and posterior muscle scars orbicular; distinct flexure running from beak to anteriormost part of posterior scar. Pallial line entire without sinus.

Remarks: Amano et al. (2001, p. 192) misinterpreted the right valve hinge as having three cardinal teeth. It has now become apparent that the "anterior cardinal tooth" is a ramp resulting from shell deformation. The "middle tooth" in their description corresponds to the real anterior one (1) which is perpendicular to the hinge base.

Comparison: Smaller specimens of *A. hamuroi* (Figure 13) have an elongate elliptical shell like *Calypptogena akanudaensis* Tanaka, 1959 (Figures 27–29 herein) from the middle Miocene Bessho Formation in Nagano

Prefecture. However, the present new species differs from *C. akanudaensis* by having a slightly higher shell with a concave ventral margin. Moreover, as the inner structure of *C. akanudaensis* is unknown, it is difficult to compare both species with each other in detail. *Adulomya kuroiwaensis* sp. nov. can be distinguished from *A. hamuroi* by having a larger shell, more anteriorly situated beak and more expanded posterior part.

Distribution: Known only from the type locality.

Paleobathymetry: *A. hamuroi* probably lived between the lower sublittoral and the upper bathyal zone, based on the associated molluscan fossils (Amano et al., 2004).

Etymology: After Mr. Toshikazu Hamuro (Imizu City, Toyama Prefecture), who collected and offered some well-preserved shells.

Adulomya kuroiwaensis Amano & Kiel, sp. nov.

(Figures 18–26)

Calypptogena sp., Ueda et al., 1995:figs. 4a–d.

Calypptogena sp. B, Amano & Kanno, 2005:208–209, figs. 8, 14–15. (*non*—figs. 7, 10).

Adulomya n. sp., Amano et al., 2010; figs. 5G, H, M, O.

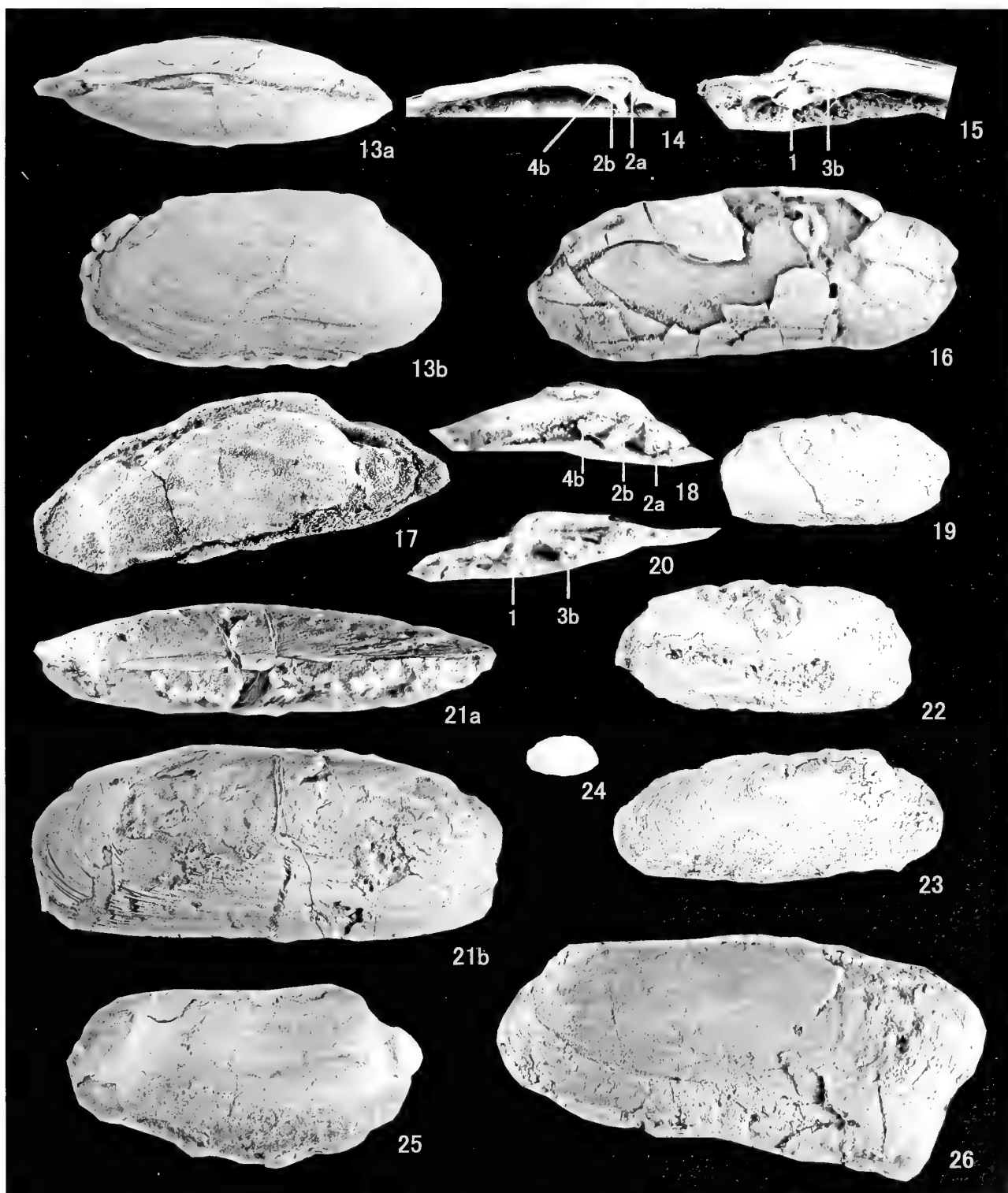
Diagnosis: A medium-sized *Adulomya* with elongate shell with anteriorly situated beak, rather straight ventral margin, expanded posterior part and no pallial sinus; two cardinal teeth in right valve; three cardinal teeth in left.

Holotype: Length 63.4 mm, height 24.8 mm, JUE no. 15858.

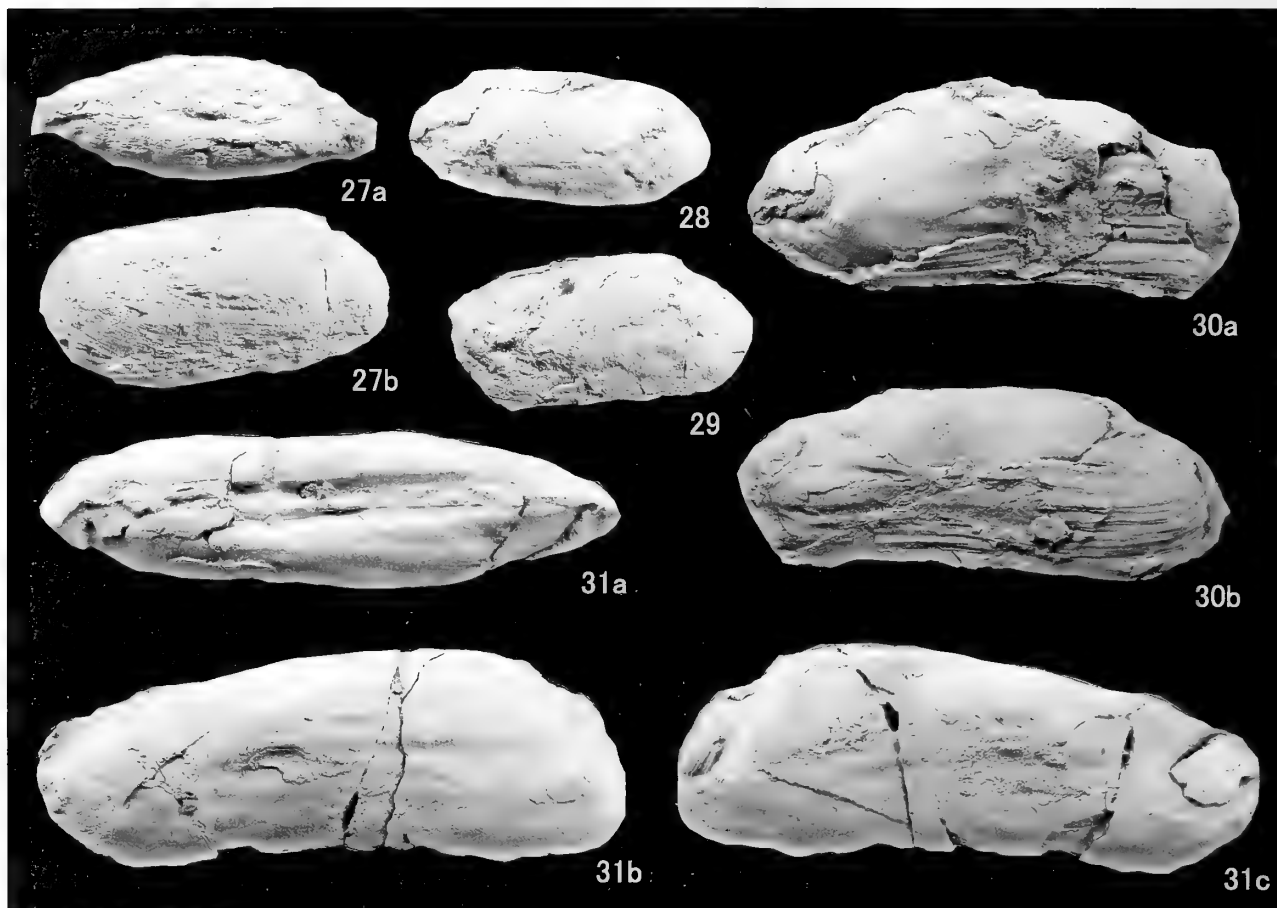
Paratypes: Length 66.7+ mm, height 24.6 mm, JUE no. 15859; length 43.6 mm, height 16.7 mm, JUE no. 15860; length 47.2 mm, height 22.1 mm, JUE no. 15861.

Type locality: There is a northern and a southern quarry at Kuroiwa in Joetsu City, Niigata Prefecture, where large carbonate bodies facing the road from Joetsu to Kashiwazaki are exposed. Of these, the southern quarry is the type locality of *Adulomya kuroiwaensis*. The exposed sediments belong to the uppermost middle or lowest upper Miocene Ogaya Formation.

Description: Shell medium in size, more than 89.1 mm long, thin-walled, elongate (height/length ratio = 0.34–0.55), posteriorly expanded, slightly inflated, equivalve and inequilateral. Surface sculptured by fine growth lines and few concentric ridges on posterior part of juvenile shell. Beak prosogyrate, situated at anterior one-eighth of entire shell length in adults and at



Figures 13–17. *Adulomya hamuroi* sp. nov. All specimens are from loc. 3. Figure 13a, b. Holotype, length 49.9 mm, JUE no. 15857. Figure 14. Left valve hinge of paratype, illustrated hinge length 31.0 mm, JUE no. 15698-3. Figure 15. Right valve hinge of paratype, illustrated hinge length 14.6 mm, JUE no. 15698-4. Figure 16. Outline of paratype, length 59.2 mm, JUE no. 15698-6. Figure 17. Paratype showing the entire pallial line and the posterior adductor scar, length 54.5 mm+, JUE no. 15698-5. Figures 18–26. *Adulomya kuroiwaensis* sp. nov. All specimens are from loc. 4. Figures 18, 20. Hinge of paratype: Figure 18, hinge

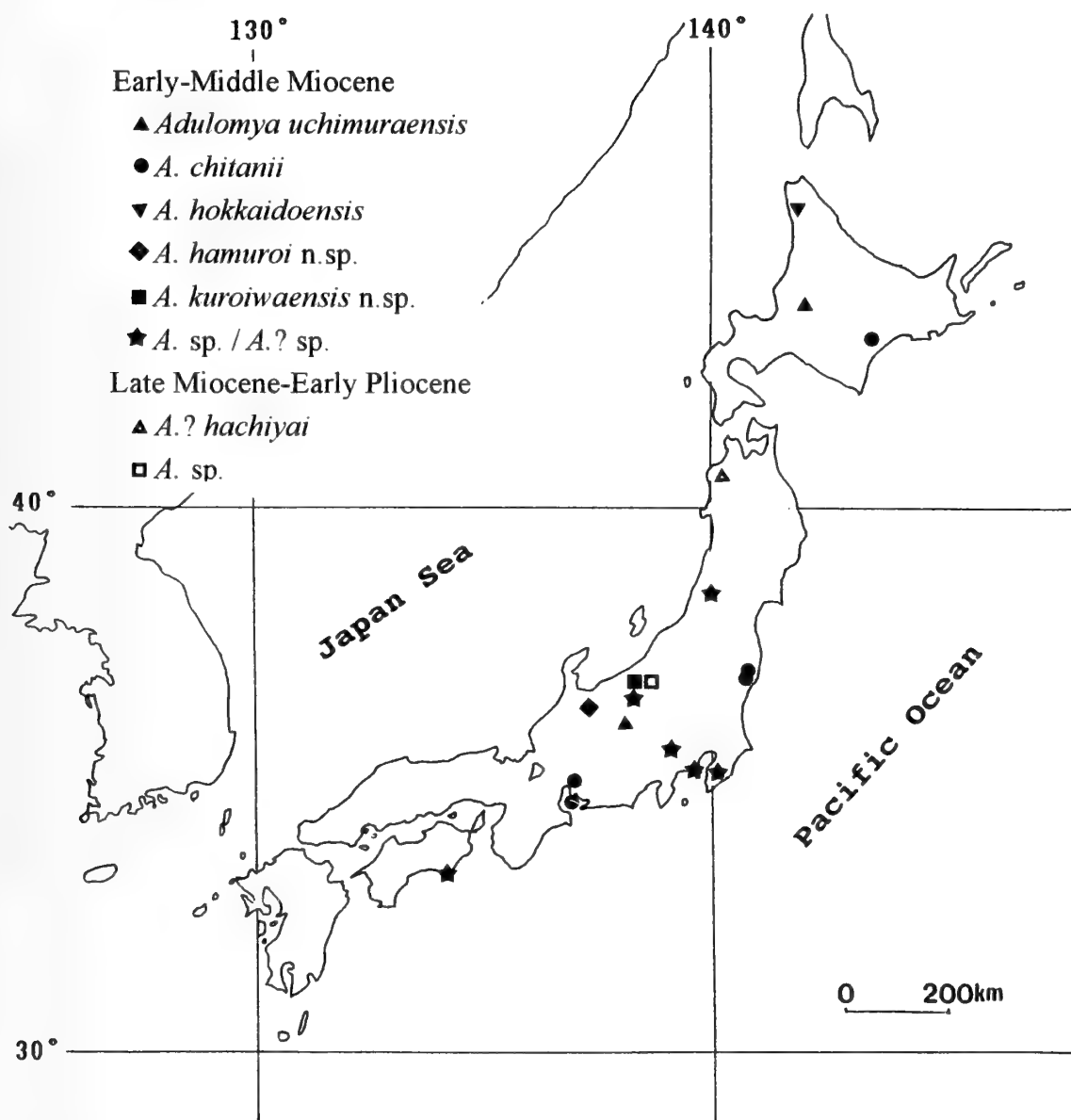


Figures 27–29. *Calyptogena akanudaensis* (Tanaka). Paratypes, loc. 1.; Figure 27a, b, length 55.7 mm, Reg. no. 426 of Tanaka (1959); Figure 28, length 43.4 mm, Reg. no. 424 of Tanaka (1959); Figure 29, length 56.2 mm, Reg. no. 425 of Tanaka (1959). Figures 30–31. *Akebiconcha uchimuraensis* (Kuroda) by Matsumoto & Hirata (1972) (= *Adulomya*? sp.), loc. 5. Figure 30a, b, outline of shell, length 93.1 mm+, NSM PM13227. Figure 31a, dorsal view showing very long external ligament; Figure 31b, right valve with entire pallial line; Figure 31c, left valve, showing deeply excavated anterior adductor scar; length, 112.5 mm+, NSM PM13228.

anterior one-sixth in juveniles. Ligament rather strong, occupying more than half of posterodorsal margin. Posterodorsal margin beneath ligament straight and horizontal, forming blunt angle with the broadly arcuate posterior half; posterior margin well rounded, graduating into ventral margin; ventral margin usually straight but concave centrally in gerontic specimen; anterodorsal margin short and broadly arcuate, graduating to narrowly rounded anterior margin. Lunule

and escutcheon absent. Hinge plate narrow with two cardinal teeth in right valve and three cardinal teeth in left valve. Subumbonal pit unknown. Right valve hinge: anterior cardinal tooth (3a) reduced; posterior cardinal tooth (3b) low, oblique posteriorly; central tooth (1) thin, perpendicular to hinge base. Left valve hinge: anterior cardinal tooth (2a) small, oblique anteriorly; middle tooth (2b) weakly bifid, slightly oblique posteriorly; posterior tooth (4b) thin. Anterior

length 9.9 mm, JUE no. 15864; Figure 20, hinge length 16.5 mm, JUE no. 15862. Figures 19, 22, 24. Outline of juvenile shells; Figure 19, length 30.8 mm, JUE no. 15867-2; Figure 22, length 40.8 mm, JUE no. 15867-1; Figure 24, length 9.8 mm, JUE no. 15867-8. Figure 21a, b; Figure 21a, dorsal view of holotype, showing external ligament; Figure 21b, lateral view of holotype, length 63.4 mm, JUE no. 15858. Figures 23, 26. Outline of paratype; Figure 23, length 43.6 mm, JUE no. 15860; Figure 26, length 66.7 mm+, JUE no. 15859. Figure 25. Paratype showing the posterior adductor scar and the entire pallial line, length 47.2 mm, JUE no. 15861.

Figure 32. Distribution of *Adulomya* in Japan.

adductor muscle scar ovate and deeply excavated; posterior adductor muscle scar subround. Pallial line entire, starting at base of anterior muscle scar, entire. Interior radial striation absent.

Remarks: From the type locality, Ueda et al. (1995) illustrated some small specimens of this species as *Calypptogena* sp. Amano & Kanno (2005) described *Calypptogena* sp. B from the same locality and from the lower Pliocene Kurokura Formation in Joetsu. Some but not all of these belong to *A. kuroiwaensis*: the identity of two illustrated specimens (*Calypptogena* sp. B of Amano & Kanno, 2005: figs. 7, 10) remains

uncertain because its proportions differ from those of *A. kuroiwaensis*.

Comparison: *Adulomya kuroiwaensis* resembles *A. chinookensis* (Squires & Goedert, 1991), from the upper Eocene seep carbonates of the 'Siltstone of Cliff Point' in Washington State, USA, in size and shell outline. But *A. kuroiwaensis* has a more anteriorly situated beak and a more expanded posterior part than *A. chinookensis*. The Japanese *A. uchimuraensis* and *A. chitanii* have lower shells than *A. kuroiwaensis*. In addition, *A. chitanii* has a pallial sinus, which is lacking in *A. kuroiwaensis*.

Some specimens of *Calypptogena akanudaensis* have

Table 4
Measurements of *A. kuroiwaensis*
sp. nov. from loc. 4.

JUE specimen no.	Type	Length (mm)	Height (mm)	Thickness (mm)
15858	Holotype	63.4	24.8	13.3
15859	Paratype	66.7+	24.6	—
15860	Paratype	43.6	16.7	11.2
15861	Paratype	47.2	22.1	—
15867-1		40.8	17.6	8.4
15867-2		30.8	14.6	8.2
15867-3		23.9	12.1	6.6
15867-4		56.2	19.5	—
15867-5		29.6	13.2	8.4
15867-6		18.4	9.9	5.2
15867-7		13.5	7.1	4.6
15867-8		9.8	5.4	2.9
15868-1		69.3	24.0	—
15868-2		42.1	16.7	—
15868-3		22.0	9.0	—
15868-4		74.9+	26.5	16.1
15868-5		41.7	17.1	—
15868-6		51.3+	18.4	10.7

similar proportions as *A. kuroiwaensis* (compare Figures 23 and 28) but in general, *A. kuroiwaensis* has a more anteriorly situated beak and an expanded posterior part. Only three paratype specimens of *Calyptogena akanudaensis* Tanaka, 1959 are preserved from the type locality (loc. 1 on Figure 1 herein) of the middle Miocene Bessho Formation in Nagano Prefecture. Despite intense subsequent collecting effort at this site, it has not been found again. Three type specimens deposited at the Shinshu-Shinmachi Museum are depicted here (Figures 27–29); they are articulated specimens and thus show no internal features. The identity of this species remains unclear.

Measurements: See Table 4.

Distribution: The uppermost middle or lowest upper Miocene Ogaya Formation.

Paleobathymetry: Based on benthic foraminifers (cf. Ueda et al., 1995), *A. kuroiwaensis* lived in the middle bathyal zone (1000–2000 m depth).

Etymology: After the local name, from where the type specimens were collected.

DISCUSSION

The fossil record of *Adulomya* in Japan includes five well-established species and several uncertain records (Figure 32, Table 5). They show an interesting evolutionary history of an initial radiation and subsequent

decline. The oldest occurrences of *Adulomya* that we are able to confirm are from the early Miocene. A Cretaceous record—as *Calyptogena (Ectenagena)* sp.—is in fact a solemyid (Kiel et al., 2008). Another record that could potentially be older than Miocene is '*Calyptogena* cf. *phaseoliformis*' reported by Ninomiya et al. (2007, 2008) in rocks derived from the Middle Formation of the Taishu Group on Tsushima Island. The absolute age of this formation is 30.5–18.7 Ma (Takahashi & Hayashi, 1985, 1987).

In the North Pacific fossil record, *Adulomya* first appeared in the Late Eocene of the eastern Pacific (Amano & Kiel, 2007). By the early Miocene it had spread to Japan, quite likely along the North Pacific continental slope as suggested by its presence in the early Miocene of Alaska (Kanno, 1971; Kiel & Amano, 2010, and herein). Prior to the arrival of *Adulomya* the only vesicomyid in Japan was the endemic genus *Hubertschenckia* (Amano & Kiel, 2007).

During early and middle Miocene time *Adulomya* had an impressive diversity in Japan, consisting of five species. Most of these species lived at lower sublittoral to middle bathyal depths; only *A. hokkaidoensis* lived in deeper waters. In contrast, the late Miocene to early Pliocene record is confined to only two unconfirmed species: *Adulomya?* *hachiyai* in Aomori Prefecture and *Adulomya* sp., in Niigata Prefecture. This decline coincides with the appearance of *Archivesica* and *Calyptogena* in Japan: *Calyptogena pacifica* Dall, 1891 from the upper Miocene Morai Formation in Hokkaido and from the upper Miocene Nodani Formation in Niigata Prefecture (Amano & Kanno, 2005), and *Archivesica* cf. *kawamurai* (Kuroda, 1943) from the lower Pliocene Ochiai Formation in Kanagawa Prefecture, central Honshu (Matsushima et al., 2003). From the Pliocene to Recent, both genera are widely distributed in Japan (Majima et al., 2005; Sasaki et al., 2005). Eight species of *Archivesica* and two species of *Calyptogena* live around Japan. Interestingly, the four Japanese species of *Adulomya* live in deeper water (3300–6809 m) than Japanese members of *Archivesica* and *Calyptogena* (Sasaki et al., 2005) as well as the fossil species of *Adulomya*. *Adulomya* might thus have followed an onshore–offshore trend as has been suggested for members of the vent and seep fauna in general (Tunnicliffe, 1992; Kiel & Little, 2006).

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Table 5
Doubtful species of *Adulomya* and their statuses.

Species	Reference	Formation	Age	Status	Remarks
<i>Calypptogena</i> (<i>Ectenogena</i>) sp.	Ogasawara et al. (1994); Kuramochi et al. (1999)	Aokiyama Formation	Early Miocene	<i>Adulomya</i> ? sp.	Elongate shell having the outline of extant <i>A. kaikoi</i> (Okutani & Métivier, 1986), up to 98.8 mm long, distinct ridge from beak to posterior corner, other internal features unknown.
<i>Calypptogena</i> ? sp. <i>Calypptogena</i> sp.	Ogasawara et al. (1986) Kanie et al. (1991)	Onnagawa Formation Misaki Formation.	Middle Miocene Middle Miocene	<i>Adulomya</i> ? sp. <i>Adulomya</i> ? sp.	Elongate shell, internal features unknown. Small, elongate shells (~ 10 mm length) resembling juvenile <i>A. chitanii</i> in general shape, internal features unknown.
<i>Calypptogena</i> sp. A	Amano & Kanno (2005)	Nanbayama Formation	Middle Miocene	<i>Adulomya</i> sp.	Elongate shell with two cardinals in right valve; specimens deformed, preventing identification on species level
<i>Solenya</i> (<i>Adulomya</i> ?) <i>hachiyai</i> Nomura, 1935	Nomura (1935)	Akaishi Formation	Latest Miocene To Earliest Pliocene	<i>Adulomya</i> ? <i>hachiyai</i> (Nomura)	Elongate shell like <i>A. uchimuraensis</i> , up to 190 mm long, no pallial sinus; right valve hinge with two cardinal teeth (Dr. Yukito Kurihara, personal communication). Very similar in size and proportion to <i>A. uchimuraensis</i> .
<i>Calypptogena</i> sp. B	Amano & Kanno (2005)	Kurokura Formation	Early Pliocene	<i>Adulomya</i> sp.	Large, inflated shell which beak located more posteriorly than in <i>A. kuroiwaensis</i> ; internal features unknown.
<i>Adulomya</i> (?) <i>azarie</i> Shikama, 1969	Shikama & Masujima (1969)	Ikego Formation	Pliocene	mytilid?	Large, elongate shell, 117.7 mm long, with expanded posterior part like <i>Giganitidas</i> Cosel & Marshall, 2003; internal features unknown.
<i>Vesicomya ellipsoidea</i> Kanie & Kuramochi, 2001	Kanie & Kuramochi (2001)	Shiramazu Formation	Pliocene	<i>Archivesica</i> or <i>Adulomya</i>	Very large (up to 235 mm), elliptical shell with two cardinals in right valve.

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Another New Species of the Urocoptid Land Snail Genus *Hendersoniella* (Pulmonata, Urocoptidae, Holospirinae) from Northeastern Mexico

FRED G. THOMPSON

Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800, USA
(e-mail: fgt@flmnh.ufl.edu)

AND

ALFONSO CORREA-SANDOVAL

Instituto de Tecnológico de Cd. Victoria, Cd. Victoria, Tamaulipas, Mexico
(e-mail: agutierr@uat.edu.mx)

Abstract. *Hendersoniella miquihuanae* sp. nov. (Pulmonata, Orthalicoidae, Urocoptidae) is described from high altitudes in limestone hills to the east of the Sierra Los Soldados in the state of Tamaulipas, Mexico. The genus is unique within the family by having a discoidal shell. All other genera have elongate-conical or cylindrical shells. *Hendersoniella* includes five species, each of which has a very limited geographic distribution in northeastern Mexico: *H. miquihuanae* sp. nov.; *Hendersoniella palmeri* (Dall, 1905); *Hendersoniella christmani* Thompson & Correa, 1991; *Hendersoniella lux* Thompson & Correa, 1991; and *Hendersoniella chonomphix* Thompson & Correa, 1991. The taxonomic status of the latter species is elevated from that of a subspecies of *H. lux*.

INTRODUCTION

Hendersoniella Dall, 1905 is confined to submesic and mesic mountain habitats at intermediate to high altitudes in northeastern Mexico (Figures 1, 8). Four species have been described: *Hendersoniella palmeri* (Dall, 1905); *Hendersoniella christmani* Thompson & Correa, 1991; *Hendersoniella lux* Thompson & Correa, 1991; and *Hendersoniella chonomphix* Thompson & Correa, 1991. The genus was reviewed recently by Thompson & Correa (1991). Previous to now the genus was known from the west slope of the Sierra Madre Oriental in the states of San Luis Potosí and from Nuevo León. Three species occur in San Luis Potosí and one occurs in Nuevo León. Each has a very limited geographic distribution, as is typical for species in the urocoptid subfamily Holospirinae. The discovery of a new species in Tamaulipas extends the known range of the genus to the east slope of the Sierra Madre Oriental and east of its recorded distribution. The novelty is geographically separated from *H. christmani* by 190 km to the north-northwest in Nuevo León. It is separated from the other three known species by about 200 km to the south-southwest in San Luis Potosí. Altitudinal distributions for *Hendersoniella* are as follow: *H. palmeri*, 2550 m; *H. lux*, 2150–2300 m; *H. chonomphix*, 1700 m; *H. christmani*, 1350–1900 m; and *H. miquihuanae* sp. nov., 2850 m.

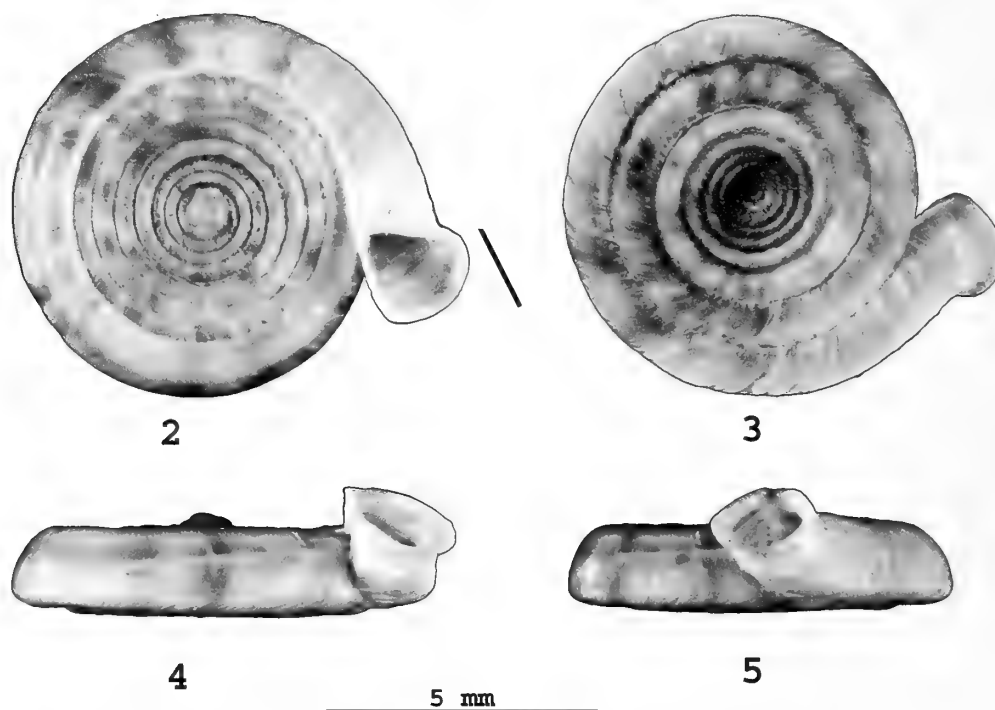
Hendersoniella miquihuanae Thompson & Correa-Sandoval sp. nov.

(Figures 2–7)

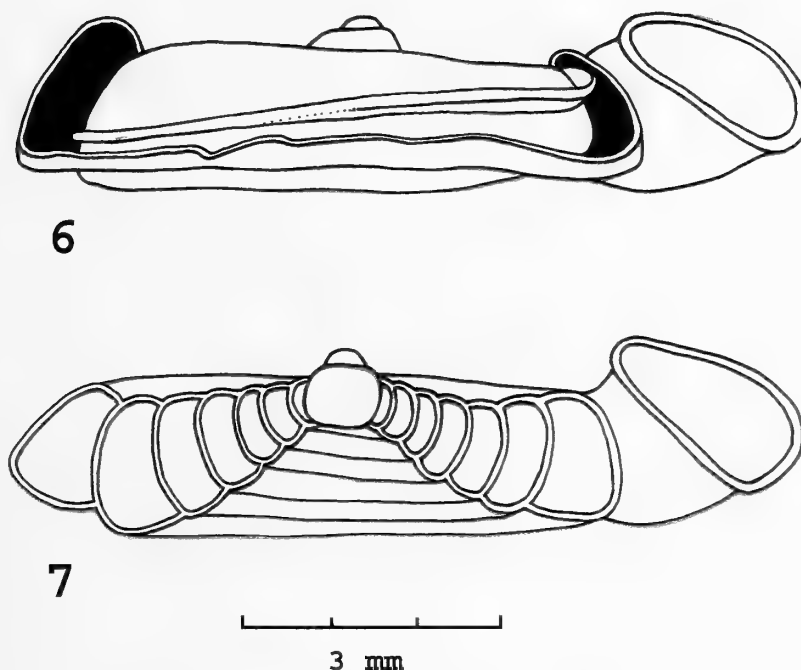
Description: The shell is discoidal in shape; thin-walled; medium sized, 7.0–8.8 mm wide behind the neck of the aperture; consisting of 9.0–9.4 whorls. The color is light gray with alternating diaphanous patches in fresh specimens. The peristome and the interior of the aperture are opaque white. The first 1.5 whorls are raised slightly above the discoidal plane of the shell (Figure 4). The last whorl ends in a neck that is deflected dorso-laterally (Figures 4, 5). The neck is moderately long, and is semitriangular in cross-section. It is directed dorso-laterally so that the aperture extends upward above the last whorl (Figure 4). The neck lacks a longitudinal impressed dorsal furrow, in contrast with other species of *Hendersoniella*. The aperture is pear-shaped as in *H. lux*. The plane of the aperture lies at an angle of about 45° oblique to the dorsal surface of the shell (Figure 5). The longitudinal axis of the aperture is aligned at an angle of about 30° to the center of the shell (black line, Figure 2). The last two whorls of the base are flat; the last whorl may ascend above the level of the penultimate whorl in some specimens (Figure 7, cross-section of shell). The



Figure 1. *Hendersoniella miquihanae* sp. nov. Habitat at the type locality viewed toward the east.



Figures 2–5. *Hendersoniella miquihanae* sp. nov., holotype, UF 415967. Figure 2. Dorsal side of shell; black bar on right shows the alignment of the axis of the aperture. Figure 3. Base of shell. Figure 4. Frontal view showing the projection of the neck and the inclination of the aperture. Figure 5. Lateral view of shell.



Figures 6–7. *Hendersoniella miquihuanae* sp. nov. Figure 6. Position of the columellar lamella within the last whorl (paratype, UF 388796). Figure 7. Transverse section through shell (paratype, UF 388596).

umbilicus is deep and funnel-shaped, and is bounded by the penultimate whorl (Figure 7). The umbilicus is about 0.36–0.44 times the width of the shell as measured across the inner perimeter of the penultimate whorl. The shell contains 9.0–9.4 whorls, and is about 7.0–8.8 mm wide. The periphery of the shell is obtusely angular and lies at the base of the last whorl (Figures 4, 5). The suprapерipheral side of the last whorls is nearly flattened. The whorls are more rounded on the ventral surface, although the outermost two whorls of the base are nearly flat. The first two whorls are smooth. The following whorls are sculptured with irregular, and sometimes white, incremental striations, which are more strongly developed around the neck of the aperture. The suture is moderately impressed on the dorsal surface, and is more deeply impressed on the ventral surface. The strong columellar lamella is visible through the shell (Figures 4, 5). It is about one whorl in length, high, deeply immersed, curving dorsally, and almost touching the dorsal wall of the last whorl (Figure 6). The anterior end of the columellar lamella terminates at one-third of a whorl behind the aperture. It is marked with longitudinal white lines.

Measurements based on the holotype and 14 paratypes (Florida Museum of Natural History [UF] 388550) selected to show variation are shown in Table 1.

Type locality: Tamaulipas, Municipio de Miquihuana, road to Nuevo León, east of the Sierra Los Saldados,

7.8 km NW of Valle Hermosa, 23°42'07"N, 99°49'36"W; 2735 m alt. Holotype: UF 415967; collected October 25, 2007, by Alfonso Correa-Sandoval. Paratopotypes: UF 388532 (7), February 21, 2006; UF 388544 (3), February 21, 2006; UF 288546 (11), May 11, 2006; UF 338547 (1), May 11, 2006; UF 388548 (5), May 11, 2006; UF 388550 (14), August 30, 2006.; UF 420746; October 25, 2007 (5).

Additional specimens are deposited in the UF; the Instituto de Biología, Universidad Nacional Autónoma de México; and in the Instituto de Tecnológico de Ciudad Victoria.

The type locality lies in limestone hills that are dominated by a sparse submesic shrub forest consisting of palms, small oaks (*Quercus* sp.), *Yucca* sp., and izotal (*Dasylirion* sp.), with an understory of patches of lechuguilla (*Agave lechuguilla*), occasional cactae, and herbaceous vegetation (Figure 1). Annual precipitation averages 500 mm (INEGI, 1985). Snails were found in limestone crevices under loose rocks and talus, but they were not uniformly distributed over the immediate area of the type locality, nor were any found at other nearby localities that appeared to have appropriate habitat. *Hendersoniella miquihuanae* was associated with another urocoptid, *Propilsbrya* sp., and a spiraxid, *Guillarmodia* (*Proameria*) sp.

Comparisons: The shell is discoidal as is *H. palmeri* (Dall, 1905) with a very flattened dorsal surface in which only the embryonic whorls protrude above the

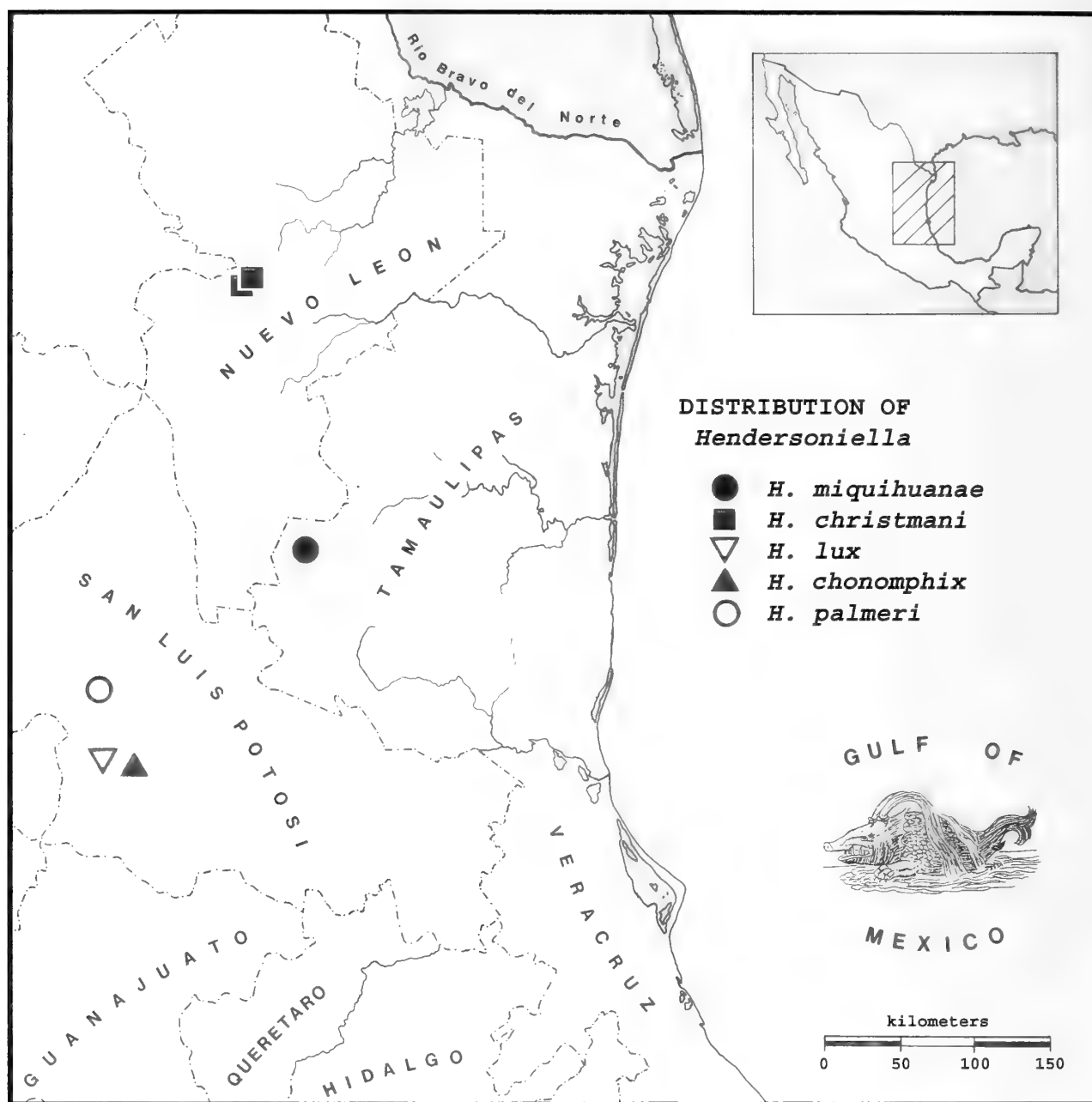


Figure 8. Distribution of *Hendersoniella* in northeastern Mexico.

planes of the last whorl. The periphery is obtusely angular at the base of the last whorl. In other *Hendersoniella* the periphery is acutely angular in comparison (Thompson & Correa, 1991). In *H. christmani* the periphery lies at the base of the last whorl, as it does in the new species. In *H. lux* and *H. palmeri* the periphery lies at or above the middle of the last whorl. The neck of the aperture projects upward

beyond the level of the apical whorl, in contrast with *H. palmeri*, in which the aperture projects dorso-laterally, but not above the level of the last whorl. In *H. lux* and *H. christmani* the aperture projects dorsally, as it does in the new species. The aperture is pear-shaped with the longitudinal axis lying at about 30° to the transverse axis of the shell, similar to *H. christmani*. In *H. palmeri* and *H. lux* the longitudinal axis of the aperture is

Table 1

Measurements based on the holotype and 14 paratypes (UF 388550) of *Hendersoniella miquihuanae*.

Specimen	Height	Width	Umbilicus	Whorls	µm/width
Holotype	2.1	8.1	3.1	9.3	0.42
Paratypes					
Minimum	1.8	7.0	2.8	9.0	0.36
Maximum	2.4	8.8	3.5	9.6	0.47
Mean	2.13	8.13	3.37	9.25	0.40
STD	0.17	0.56	0.31	0.23	0.03

tangential to the spire. The columellar lamella is about one whorl in length, thereby being more than twice as long as it is in other *Hendersoniella*. The shell wall is thinner than it is in other species.

Earlier we referred to the internal lamella as the parietal lamella (Thompson & Correa, 1991). We now consider the structure to be the columellar lamella. The columellar lamella is a basic structure in most other genera of the Holospirinae. Those species that possess internal lamellae always have a columellar lamella, and the columellar lamella, when present, is the first to develop ontogenetically (Thompson & Mihalcik, 2005). In *Hendersoniella* the lamella occupies the same relative position within the shell as does the columellar lamella in other genera, and it is the only lamella to develop.

Previously we treated *Hendersoniella chonomphix* as a subspecies of *H. lux*. *Hendersoniella lux* has a well-developed columellar lamella. *Hendersoniella chonomphix* lacks such a structure. Because of its absence we now consider this trait to be specifically significant, and

we treat *H. chonomphix* as a specific species from *H. lux*.

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